A REVISION OF THE APHID GENUS *ESSIGELLA* (HOMOPTERA: APHIDIDAE: LACHNINAE): ITS ECOLOGICAL ASSOCIATIONS WITH, AND EVOLUTION ON, PINACEAE HOSTS

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Abstract. —This revision recognizes 13 species, 2 subspecies, and 3 subgenera of *Essigella* aphids of the lachnine subtribe Eulachnina. *Essigella* (*Archeoessigella*) NEW SUBGENUS, *Essigella* (*Lambersella*) NEW SUBGENUS, *E.* (*L.*) *eastopi* NEW SPECIES, *E.* (*L.*) *hillerislambersi* NEW SPECIES, *E.* (*E.*) *critchfieldi* NEW SPECIES, and *E.* (*L.*) *fusca voegtlini* NEW SUBSPECIES are described. The taxonomic status is changed for *E.* (*E.*) *knowltoni braggi* Hottes NEW STATUS, *E. agilis* Hottes NEW SYNONYM, *E. claremontiana* Hottes NEW SYNONYM, *E. cocheta* Hottes NEW SYNONYM, *E. gillettei* Hottes NEW SYNONYM, *E. maculata* Hottes NEW SYNONYM, *E. monelli* Hottes NEW SYNONYM, *E. oregonensis* Hottes NEW SYNONYM, *E. palmerae* Hottes NEW SYNONYM, *E. patchae* Hottes NEW SYNONYM, *E. pergandi* Hottes NEW SYNONYM, *E. pineti* Hottes NEW SYNONYM, *E. robusta* Hottes NEW SYNONYM, and *E. swaini* Hottes NEW SYNONYM. A phylogenetic tree for the genus is reviewed; that estimate, which used *Pseudessigella* as a outgroup and employs evolutionary quantitative genetic rationales, was produced using discriminant function analysis and a maximum-likelihood networking algorithm, because conventional cladistic characters were inadequate within the genus. The phylogeny is corroborated because it closely reflects the genetic relationships of the aphid's Pinaceae hosts, and their biogeographic origins. *Essigella* appear to have evolved with their hosts, or in a resource-tracking fashion, and seem to display instances of character-displacement among closely related species in (or near) sympatry, presumably as a result of competition of their host pines as resources.

Key Words. —Insecta, phylogeny, host associations, character displacement, evolutionary quantitative genetics

This study addresses the systematics, phylogeny and host associations of *Essigella.* The genus, one of three composing the subtribe Eulachnina (Lachninae: Cinarini), is restricted to North America and is the only native Nearctic group of the subtribe. *Essigella* are linear-bodied and feed on the needles of Pinaceae, chiefly *Pinus* but also *Pseudotsuga* and *Picea.* They are solitary aphids that move quite rapidly when disturbed; several may group facultatively near the base of a needle, where they may be tended by ants. Cage studies of individual aphids (unpublished data) on marked needles indicated that adult virginoparous apterae of *Essigella* readily wander over pine branches.

Essigella is often most abundant early in the season (Burke 1937), and may damage pines (Turpeau & Remaudiere 1990). However, its populations may lower by summer, making the needle yellowing that it causes difficult to diagnose (Brown & Eads 1967). In the southeastern U.S., *Essigella* density peaks between September and March, and falls to its lowest level during June through August (Patti & Fox 1981a), although outbreaks have occurred in May and June (Hood & Fox 1980). *Essigella* seem to occur most heavily on young trees, particularly on the lower east side (Patti & Fox 1981b), which has afternoon shading. In the west, *Essigella*

occasionally damages Christmas tree plantations (California Department of Food & Agriculture, unpublished data). Sampling (Hood & Fox 1978) and control regimes (Hood & Fox 1980) have been developed for *Essigella* in southeastern U.S. lumber plantations.

Eastop & Hille Ris Lambers (1976) list 21 species in the genus. *Lachnus californicus* Essig (1909) was the first described species, but immediately thereafter Del Guercio (1909) described the genus *Essigella*, with *L. californicus* Essig as its type species. A second species, *E. pini* Wilson (1919), was described a decade later, with two more, *E. fusca* Gillette & Palmer (1924) and *E. hoerneri* Gillette & Palmer (1924), following shortly thereafter. The genus then sat taxonomically dormant until its synopsis by Hottes (1957), in which 16 new names were created [*E. agilis* Hottes, *E. braggi* Hottes, *E. claremontiana* Hottes, *E. cocheta* Hottes, *E. essigi* Hottes, *E. gillettei* Hottes, *E. knowltoni* Hottes, *E. maculata* Hottes, *E. monelli* Hottes, *E. palmerae* Hottes, *E. patchae* Hottes, *E. pergandi* Hottes, *E. pineti* Hottes, *E. robusta* Hottes, *E. swaini* Hottes, *E. wilsoni* Hottes]; another name, *E. oregonensis* Hottes (1958), was added a year later.

While working on aphids in California during the 1960s, D. Hille Ris Lambers attempted to treat *Essigella.* He concluded (unpublished notes) that the only available key (Hottes 1957) to *Essigella* did not work for numerous reasons, and that the genus needed a major revision using similarly cleared and mounted specimens. In 1978, he advised me (D. Hille Ris Lambers, personal communication) that the systematics of *Essigella* was extremely difficult, and that he ranked the genus as one of the most taxonomically problematic among aphids. Since then, I have analyzed the biological groups in *Essigella* in relation to their hosts (Sorensen 1983), suggested a phylogeny (Sorensen 1987a), described three new species (Sorensen 1988), analyzed the cladistic placement of the genus among the Eulachnina (Sorensen 1990), assessed phylogenetic changes in shape component variance between *Essigella* and its sister group (Sorensen 1991), and presented analyses deciphering the biological groupings of *Essigella* on *Pinus contorta* Douglas (Sorensen 1992a).

The problems of *Essigella*'s systematics are due to the exceptional reduction of morphological attributes, over that of an already neotinous subtribe (Sorensen 1990). Retained features in the genus are either extremely variable and overlapping among species, represent reductions, or involve pigmentation suites, which often run counter to morphology, and that grade from fully expressed to absent within populations. In addition, several instances of character displacement seem to occur among closely related species under sympatry, or near sympatry (Sorensen 1992a, unpublished data). Discrete characters are unusual within the genus, which shows many internal homoplasies and few conventional autapomorphies or reliable synapomorphies (Sorensen 1987a). In *Essigella,* many characters have transformations that are nebulous and unusually difficult to polarize. Traits that are considered taxonomically meaningful in the genus are often more typical of intraspecific variation in other lachnines, and the converse is also true. Therefore, interspecific variance in *Essigella* seems to be antipodal to that encountered among many other closely related aphids; traits that might be considered to be indicative of close relationships within the genus, often turn out to show merely superficial resemblance because of homoplasy, intraspecific variance or apparently faulty ontogenic physiognomy.

Attempts to determine character plasticity in *Essigella,* by culturing under variable environmental conditions in the laboratory, failed for several reasons. These aphids, in contrast to others, often could not be successfully transported to the laboratory from field. Those *Essigella* brought to the laboratory alive were difficult to rear and transfer among host plants. Their laboratory manipulation was hampered by their solitary, but mobile, habits; to be located, specimens often had to be jarred from the needles of their host, and frequently did not reestablish on the plants; a trait noted by Hottes (1957). Electrophoretic analysis of field collected samples was also problematic: assessing potentially mixed field populations was difficult because morphological differences among species were not yet understood, and isozymic responses were unclear.

This revisionary research was based upon newly collected material with proper host associations from throughout most of the range of the genus, following a suggestion from D. Hille Ris Lambers (personal communication). In conjunction with the more traditional approaches to aphid systematics, multivariate analyses were necessary to determine intra- and intersample variation. Ultimately, previously existing *Essigella* material was studied and fit into the derived taxonomic scheme without incident. This approach allowed an unbiased initial view of the genus, which I believe was a prerequisite to its successful revision.

METHODS AND PHILOSOPHY

Collection and Processing of Specimens. — All potential *Essigella* hosts, including all conifer genera, were sampled during 1977–1979 for this revision (Sorensen 1983). Collections were made from major geographic populations of the aphids' hosts throughout western North America, north of Mexico (see Critchfield & Little 1966); of these, over 340 host/sites yielded *Essigella.* Over 7000 specimens, with an average of over 20 per collection, were collected, processed and studied; additionally, existing material was borrowed from depositories. Elsewhere, I have listed all locations, with host associations, where my sampling found *Essigella* (Sorensen 1983: appendix A1), and have provided a distribution map of all sampling locations (Sorensen 1983: figs. 1.1, 1.2).

Hottes' (1957) *Essigella* specimen processing was poor and resulted in the obscuring of characters or their erroneous interpretation (e.g., Hottes 1957: 108, key couplet 1, "tarsal claws not distinctly bifurcated"). As stressed by D. Hille Ris Lambers (unpublished notes, personal communication), during this project I have processed and mounted all *Essigella* specimens using standardized clearing and mounting techniques. Preparation followed Hille Ris Lambers (1950), and required sequential boiling in: (a) 95 percent ethanol [5 min], (b) 10 percent potassium hydroxide [4 min], and (c) saturated chlorophenol until the body contents were translucent [ca. 7–8 minutes]. Treatment times are important for preservation and standardization of subtle pigmentation differences. Processed specimens were mounted immediately (or rarely stored up to 1 week in chlorophenol) in Hille Ris Lambers medium (gum arabic 12 g, concentrated glycerine 6.5 g, chloralhydrate 20 g, distilled water 20 cc). Slides were thick (deep), thus minimizing common compression artifacts for body width measurements. Immediately after mounting, collection numbers were etched into the slides to prevent any mix-up of samples before labeling.

Analytical Methods. — In addition to conventional analytical techniques used in aphid systematics, Sorensen (1983) conducted multivariate analyses to circumscribe the biological groupings of *Essigella.* Those multivariate analyses were restricted to adult viviparous apterae to limit the influence of seasonal polymorphism and developmental trait variation. Inadequate availability prevented the separate analysis of other morphs. Initially, only *Essigella* collected from natural stands of native hosts were analyzed to limit potentially confusing environmentally induced variation; later, *Essigella* from planted stands and nonnative hosts were incorporated without incident.

For analysis, individuals from samples were first divided into initial groups by host and geographic location. These initial groups were then circumscribed using ordination analyses to establish common covariant character patterns among both the individuals and groups, and to determine the interrelationships among the initial groups. In the original, exploratory analyses (Sorensen 1983), several subset combinations of up to 66 morphometric characters were employed; these were later reduced to a 26 character subset (see Sorensen 1991: table 1) that was used to circumscribe all final biological groups within the genus.

Quantitative analyses of the initial groupings involved the following steps: (1) exploratory delimitation of relationships using principal component analysis [Duncan & Phillips 1980: program PNCOMP] and clustering techniques [Duncan & Phillips 1980: programs GRAPH and CLUST], followed by reassessment of the groupings into biological groups; (2) bivariant plotting of various characters for the deduced biological groups using extended data sets to determine the simplest character combinations that best allow their separation; (3) corroboration of inter- and intragroup variance, using the deduced biological groups as "knowns" in discriminant function analysis [Nie et al. 1975: SPSS, version 7, program DISCRIMINANT, direct selection mode, Wilks-λ criterion]. Sorensen (1992a) details an example of the use of these procedures in deciphering biological groupings in a species complex within *Essigella.* After the final biological groups were assessed, they were cladistically verified, wherever possible, by establishing conventional autapomorphies or synapomorphies with reference to out-groups (see Sorensen 1990). Ultimately, a phylogenetic tree was produced for *Essigella* (see phylogenetic analysis section).

With respect to the ordinations used (Sorensen 1983), populations of parthenogens can cause problems when assessing their demarcations into groups. Because aphid clones within samples could not be practically ascertained, exemplars were employed in this project. Normally, these were restricted to a single individual per sample. This prevented reduction of effective statistical sample size (*n*); it thus minimized the miscalculation of intragroup genetic variance, because only environmental and error components are left to account for observed intragroup dispersions around centroids as samples become saturated with identical genotypes. False low estimates of intragroup genetic variance cause overestimation of intergroup divergence and phyletic anagenic distance (Sorensen 1987b).

Operational Species Concepts Employed. — Determining aphid species, in general, is often problematic because of their anholocyclic lineages, which often survive indefinitely in noncontinental climates. I consider an *operational aphid species,* sensu Doyen & Slobodchikoff (1974), to be those recombinant individuals or parthenogenetic populations that share a unique phyletic lineage. This is pref-

erably recognized by a conventional autapomorphy. Alternatively, lineages may be deduced from their congruity of conventional diagnostic synapomorphies or, if necessary, plesiomorphies, provided they are genetically stable (not induced by abiotic factors). If nonautapomorphies must be used to deduce a species, its populations also must show common distributional and host coincidence; additionally, species must be multivariately circumscribed following the evolutionary quantitative genetic logic outlined in Sorensen & Foottit (1992), using principal component and discriminant function analyses (e.g., Sorensen 1992a: figs. 3 and 6).

Here, subspecies are recognized only when they impart ecologically or evolutionarily relevant information; they denote divergent or distinct allopatric *geographic* populations (sensu Mayr 1969). This differs from a common usage in aphid systematics, where a subspecies is often named to denote the sympatric variance shown by phenotypically deviant individuals, sometimes on the same host. I consider an *operational aphid subspecies* to be allopatric and show either: (a) tighter agglomeration in clustering analyses (e.g., Sorensen 1992a: GRAPH analyses), or (b) a more restrictive distribution in the attribute space of ordinations, than do their species within analyses of species-groups (e.g., Sorensen 1992a: fig. 3, as the SNV vs. CAS and RMT distribution in PCA-1).

Taxonomic Key Usage. — The key to *Essigella* species requires adult viviparous apterae (subgenital plate present and entire, gonapophyses and siphunculi present) and, in some instances, their ultimate stadium nymphs (subgenital plate and gonapophyses absent, abdominal dorsum membranous with distinctly demarcated plates at dorsal setal bases). Because *Essigella* species are exceptionally variable, with overlapping interspecific variation in many traits, calculations of discriminant functions (DF), based on several characters, are sometimes required for morphologically based identification. The key appears to have a reliability of at least 90%; host plant information is included for more positive identification.

Because of references to subtle pigmentation differences and DF calculations, remounting of some existing slides may be necessary to use the key. Referral to paleness or pigmentation in the keys, diagnoses or discussions throughout this work are to slide mounted material. Slides must be properly cleared, noncompressed, and mounted so that the sagittal plane of the aphids is oriented perpendicular to the slide. Intrapopulational variance in *Essigella,* or varying slide preparations, will require that you judge a circumstance in a key couplet to advance by alternative routes. If you are unsure when asked about the degree of specimen pigmentation or slide compression, elect the nonpigmented or compressed slide option. Questions about pigmentation of the body dorsum refer to the background intensity, exclusive of setal bases or muscle attachment plates. Slide compression should be judged conservatively; it is most apparent as a distortion (widening) of the outline of the head, anterad of the eyes, or the rostral base. (Although body widths, especially head width, are important in *Essigella,* they are generally not used, or are minimized [with warning], in the key due to compression or orientation faults in many slides.) When asked the number of setae on abdominal tergum VIII, or the number and pattern of dorsal setae on abdominal terga III–IV, compare several specimens and use the mode (the latter can be most easily distinguished on ultimate stadium apterae nymphs, where each seta is on a scleroite).

DFs are required for specimens whose trait variance occupies an interspecific

overlapping range; couplets requiring DFs occur only after those based on non-overlapping variation. DF calculation requires (a) the measurement of several characters, (b) the multiplication of each by a given coefficient, (c) the summation of all resulting products, and (d) the addition of a constant [for adjustment]. This grand sum represents a discriminant score (D.S.), whose value represents a threshold figure for classification of an individual. Where DFs are required, for optimal classification their scores must be calculated to five figures after the decimal, and be based on measurements in mm to three figures after the decimal; the latter may require magnifications of 300–400×, and error of as little as 5% can result in misclassifications.

Presentation of Taxonomic and Distributional Data. — The sequence of species descriptions in this revision reflects their phylogenetic order. Variability and phenotypic similarity among *Essigella* species preclude their illustration here, except for a schematic topological map of dorsal setal positions on the abdominal terga; my previous *Essigella* illustrations (i.e., Sorensen 1988: figs. 1–3; 1991: fig. 1) show only that these aphids are relatively linear, varying somewhat in width, or that traits are variable (Sorensen 1991: fig. 2). The keys provided are the most reliable means of identification.

I consider all taxonomic names indicated to be new as being legally and originally described here; previously, they were considered to be manuscript nomens in Sorensen (1983), a thesis that is unpublished for nomenclatural purposes under nomenclatural rules (ICZN 1985: Articles 8-A1, 8-A3, 8-B, and presently 8-C, 9-2, 9-3, 9-4 and 9-6).

Distributional data are listed for each species: use of "JTS" under material examined indicates J. T. Sorensen as the collector. Distributional maps for *Essigella* species depict data locales, differentiated as JTS vs. nonJTS collections, superimposed over host ranges; the latter were derived from Critchfield & Little (1966), Little (1971), and Griffin & Critchfield (1972).

Abbreviations and Depositories. — My coded references to *Essigella* taxa elsewhere (Sorensen 1983, 1987a, 1992a, b) are listed at the end of each of the sections for each taxon. The U.S. National Museum of Natural History, Washington, D.C., is represented as NMNH. The Canadian National Collection, Agriculture Canada, Ottawa, Ontario, is represented as CNC. Several of Essig's types are deposited in the Essig Museum of Entomology, at the Department of Environmental Sciences, Management and Policy, University of California at Berkeley; in 1993, that department was created through an amalgamation of several others, including the Department of Entomological Sciences, which formerly housed the Essig Museum.

CHARACTER DISCUSSION

Essigella are extremely variable aphids. Their normal character variation is discussed under each species or subgenus, as are some transformations, synapomorphies and autapomorphies. This section concentrates on the definitions and phylogenetic transformations of traits; diagnostic autapomorphies are not discussed here unless they show intraspecific variation or represent an independent state within a transformation series with multiple states.

Aberrations. — Rare *Essigella* individuals exhibit aberrant traits that are virtually always expressions of plesiomorphic states that should not occur on their species (e.g., the number of dorsal hairs on the abdomen). This probably reflects the

failure of regulatory genes that normally suppress plesiomorphic phenotypic expressions, which is more likely than new creation of a derived state; the suppressed plesiomorphy, already encoded in the genome, requires merely a gene failure for expression. There also appear to be similar suppression failures involving ontogenic phenotypes, where traits of one stage or morph show up erroneously on another (e.g., allometric differences in relative appendage length). Hottes (1957) sometimes erroneously considered such individuals to be new species.

Fusion of Terga.—Sorensen (1983 [data used in 1987a], 1988, 1990, 1991, 1992a) previously had misinterpreted the fusion of the meso- and metanota, and demarcation of abdominal tergum I in *Essigella*. The correct interpretation of fusion of the dorsum in *Essigella* is: head + pronotum fused, meso + metanota fused, abdominal tergum I free (except *E. essigi*), abdominal terga II–VII fused, abdominal tergum VIII free. Previously, I thought the meso + metanotal fusion was solely the mesonotum, abdominal tergum I was the metanotum, and abdominal terga I–VII, instead of II–VII, were fused. This error was discovered when R. L. Blackman (personal communication) suggested that the autapomorphous tergal fusion in *E. (E.) essigi* involved abdominal tergum I, rather than the metanotum. With the exception of species descriptions in Sorensen (1988), corrected here, this reinterpretation does not affect the conclusions of any of those studies; because only the relative definitions of characters, not data, were erroneous. It does mean, however, that the meso + metanotal fusion in *Essigella* is an additional synapomorphy for the genus, beyond those listed in Sorensen (1990); a meso-metanotal demarcation line is evident in *Pseudessigella*.

The character definitions in error previously are corrected here, as: old 'number/ [code] definition *error*' > *correction*; but {comments} may be injected or substituted for full definitions. Sorensen (1983, 1991: table 1): '12/[L2THOR] {length of *mesonotum*}' > *fused meso + metanota*; '13/[L3THOR] {length of *metanotum*}' > *abdominal tergum I*; '15/[LVABSC],' '16/[NHAB2DT]' and '17/ [NHAB2M]' {all on abdominal segments *II–IV*} > *III–V*. Sorensen (1990: table 1): '17/abdominal terga *1–7*' > *2–7*. Sorensen (1992a: table 2): '3/*mesothoracic* terg. L' > *fused meso + metathoracic*; '7/*metathoracic terg.* L' > *abd. seg. 1*; '10/ *abdomen* {segments 1–7} L, excluding seg. 8' > *abdomen seg. 2–7* L; '25/marginal seta L on *metathorax*' and '54/W between most-mesal pair of dorsal (spinal) setae on *metanotum*' > *abd. terg. 1*; '28/dorsal (spinal or pleural) seta L on abd. terg. 2' and '29/marginal seta L on abd. terg. 2' > *3*; '30/ventral seta L on abd. seg. 2,' '41/spiracular plate L on abd. seg. 2' and '57/spiracular plate W on abd. seg. 2' > *3*; '40/L of presiphuncular abd. {including segment 1}' > {add} *excluding abd. seg. 1*; '44/sagittal L of largest ventral abd. sclerite on seg. 2–4,' '45/L of dorsal (spinal or pleural) setae between dorsal muscle attachment plates on abd. seg. 2–4,' '46/N of dorsal (spinal or pleural setae between dorsal muscle attachment plates on abd. seg. 2–4' and '58/largest ventral abd. sclerite W on seg. 2–4' > *3–5*.

Sclerotization.—Sclerotization is not equivalent to pigmentation, although sclerotized areas usually are at least somewhat pigmented. Here, it is the color independent distinctiveness or thickness of a body surface in comparison to an adjacent membranous area, as is evident in *Essigella*'s tergal fusions.

The abdominal dorsum of adult viviparous apterae of *Essigella* is sclerotized, in contrast to the other genera of the Eulachnina (Sorensen 1990). This scleroti-

zation is universally present in all adults of that morph, although pigmentation may be quite pale, making it sometimes virtually impossible to detect. When adult viviparous apterae of *Pseudessigella* and *Eulachnus* are superficially compared to *Essigella,* they resemble the latter's ultimate nymphal stadia, which lack the dorsal sclerotization. In *Essigella,* the sclerotized dorsum is *what should have been* referred to as the "cape" by Hottes (1957); he used the term with reference to pigmentation for more melanic specimens, noting simply its presence or absence, despite its actual gradation. The sclerotization of the abdominal dorsum of *Essigella* seems to have occurred at the inception of the genus, and represents a synapomorphy. It has been strengthened or reduced in various lineages within the genus, and varies homoplasiously from faint to heavy within species groups.

Examination of the abdominal dorsum of later stadia nymphs of *Essigella,* versus adult viviparous apterae, best reveals the latter's abdominal sclerotization. On adults, scleroites at the base of the dorsal setae of the abdomen have been lost or reduced, probably due to incorporation into the general sclerotic field of the abdominal dorsum; at most, the remnant scleroites appear as indistinctly bordered darker areas at the setal bases (see pigmentation). In contrast, scleroites are usually prominent, with well defined borders on the membranous abdomen of nymphs and alates.

Pigmentation. — Pigmentation represents melanization, and, where quantified, is expressed here as a density equivalent to the percentage of solid black in a screen of 52 lines per centimeter (Sorensen 1983). Referral to paleness or pigmentation in the keys, diagnoses or discussions throughout this work are to slide mounted material. Although sometimes aphid taxonomists (in litt.) place little weight on minor or trivial pigmentation patterns, in aphids certain pigmentation suites — denoted here as a covariant series of patterns occurring within phyletic lineages — are more stable within species, over their seasonal polymorphic changes, than are simple length ratios for body segments (D. Hille Ris Lambers, personal communication). Often, major pigmentation suites on viviparous apterae of *Essigella* are indicative of one or several species; these are considered to be taxonomically important when they have genetic basis and are monophyletic. Unusual environmental conditions can cause variation of pigmentation intensity in aphid species, but not a change in a pigmentation suite. Consequently, reliable pigmentation is preferred here for identification, where feasible.

Unfortunately in *Essigella,* the expression of a reliable pigmentation suite that is characteristic for a species or group, can vary from strongly pigmented to completely pale within populations; whereas other *Essigella* species are always pale. Furthermore, to hamper identification, faint pigmentation in slide mounted material can be bleached by excessive clearing or prolonged exposure to sunlight. Geographic variation can also occur in pigmentation suites. For example, many minor pigmentation tendencies (e.g., subtle variations of shade or intensity of melanin) recur as homoplasies within *Essigella*; these are usually of little taxonomic interest, except in regard to intraspecific geographic variation.

Two categories of pigmentation suites can be recognized within *Essigella* for pigmented individuals of adult viviparous apterae: the expression of shading among the tibiae, and of the background of the dorsum of the abdomen or entire body. Reference to body or abdominal pigmentation in the text and keys refers only to background shading, not to darkened muscle attachment sites and setal

bases. The numerous pigmentation suites are discussed in the descriptions, diagnoses and discussions of species.

A general darkening of the body dorsum, as a homoplasious apomorphy, occurs in *E.* (*L.*) *eastopi*, *E.* (*E.*) *essigi*, *E.* (*E.*) *critchfieldi* and *E.* (*E.*) *knowltoni knowltoni*. Of these taxa, the dorsum of *E.* (*L.*) *eastopi* is considered to be an autapomorphy because it shows a unique dorsomedial lightening of the thorax and abdomen (state A). In contrast, the dorsum is evenly dark (state B) in *E.* (*E.*) *essigi*, *E.* (*E.*) *critchfieldi* and some *E.* (*E.*) *knowltoni knowltoni* (Cascade Range); however, other *E.* (*E.*) *knowltoni knowltoni* (Rocky Mountains) show a lightening of the frons and head (state C), or of the entire dorsum. The evenly paler dorsum of *E.* (*E.*) *knowltoni braggi* (state D) is assumed to be a apomorphic reversal from state C. The transformation for the trait is assumed to be A ← B → C → D.

The most useful tibial pigmentation suite involves the mesotibiae being at least subtly, and usually substantially, paler than both the pro- and metatibiae. This apomorphy is unique to *E.* (*Lambersella*), where it is present for pigmented individuals of all morphs. It can be hard to detect on some darkly pigmented *E.* (*L.*) *eastopi*, however, because their legs are quite lightened.

Hottes (1957) and Hille Ris Lambers (unpublished notes) erroneously regarded the presence or absence of pigmented spots that often surround the bases of the dorsal setae on the abdomen of adult viviparous apterae to be of taxonomic value. Instead, the spots represent intraspecific or usually intrapopulational variation in most species. They are seldom present, and then only subtly, in *E.* (*Archeoessigella*) and *E.* (*E.*) *wilsoni*. Within most species, the spots usually occur only on moderately pigmented individuals, and I suspect their expression is a remnant of a juvenile factor; they are no doubt homologous with the scleroites that are invariably present in nymphs (see sclerotization).

Abdominal Chaetotaxy. — In *Essigella,* unlike *Eulachnus* (D. Hille Ris Lambers, personal communication), the number and distributional pattern of setae on the abdominal dorsum appear unaffected by environmental factors. In a principal component analysis of all *Essigella* taxa (Sorensen 1983), the number of abdominal setae show variation that is subordinate only to general-size (component 1). These setae can be divided into three categories: (a) dorsal setae on terga III–IV, (b) marginal setae on terga III–IV, and (c) setae on tergum VIII. Within any species, the characteristic state for each of these setal categories is stable among all known morphs. Marginal setae, at least in more apomorphic states, do not appear to show the same type of intraclonal variation as has been found to be dependent upon the number of sequential generations after the fundatrix in other aphids (see Crock & Shanks 1983, Blackman et al. 1987). In this study, such variation would have been detectable as seasonally related variation within natural populations, which would be in contrast to covariant patterns of other diagnostic attributes for taxa; to date no such variation has been found.

The dorsal setae of the abdomen are defined here as those setae that occur between (mesad to) the most sagittally-oriented pair of the three muscle attachment points on each side of the dorsum of each abdominal tergum. The dorsal setae can be further broken into two groups: dorsal major setae, which occur mesally, and dorsal minor setae, which occur more laterally. These subgroupings (Fig. 1) become apparent when tracing the evolutionary transformations of the dorsal setae in the genus. Although the setae may be difficult to see in some cases,
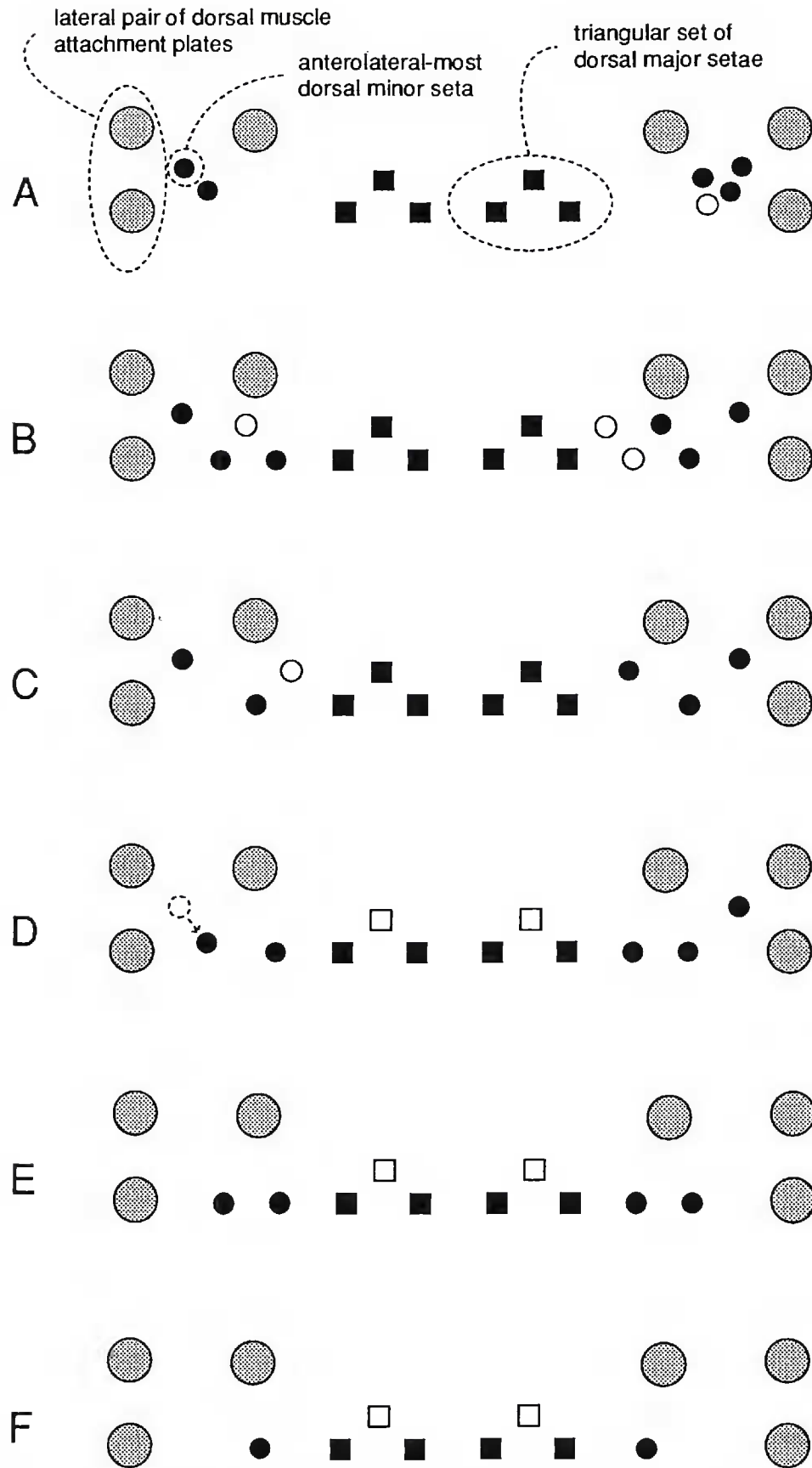
Figure 1.   Schematic maps of approximate positions of dorsal setae on an abdominal terga III and IV. See comments under abdominal chaetotaxy in the character discussion section. Maps represent typical relative setal positions, which can vary; the right and left half of each map shows the more common possible positions. Large gray circles = dorsal muscle attachment plates; each: black square = dorsal major seta, black circle = dorsal minor seta; white squares or circles (majors or minors, respectively) show other possible setal positions that are usually absent. A.—*Pseudessigella* [also see Sorensen (1991: fig. 3)]. B.—*E.* (*Archeoessigella*). C.—*E.* (*Lambersella*) expression 1 [i.e., most often *E.* (*L.*) *hillerislambersi*]. D.—*E.* (*Lambersella*) expression 2 [i.e., most often *E.* (*L.*) *fusca, E.* (*L.*) *eastopi*] (note that a anterolateral-most dorsal minor may move posteromesally). E.—*E.* (*Essigella*) expression 1 [e.g., *E.* (*E.*) *essigi, E.* (*E.*) *wilsoni, E.* (*E.*) *alyeska, E.* (*E.*) *critchfieldi, E.* (*E.*) *knowltoni*]. F.—*E.* (*Essigella*) expression 2 (e.g., *E.* (*E.*) *californica, E.* (*E.*) *hoerneri, E.* (*E.*) *pini*]. Transformation: A → B → C/D → E → F.

they are usually well defined and easily traced in the later stadium nymphs of viviparous apterae (and their adults in *Pseudessigella*), where they occur on scleroites in the membranous field of the abdominal dorsum.

In *Pseudessigella* (Fig. 1A; Sorensen 1991: fig. 3), the dorsal majors occur as two bilateral, but mesal, groups of three triangularly-arranged setae that flank the mid-line. Each triangular group has one setae to the anterior and two that flank it to the posterior. The dorsal minors occur as one to several smaller setae that are anterolaterad to the dorsal majors. They are posteromesad to the anterad plate of the sagittally-oriented muscle attachment plates on each segment side (i.e., the anterolaterad of the three plates). Apparently at least one dorsal minor seta remains in this position, relative to that muscle attachment plate, throughout the transformations among the more plesiomorphic *Essigella.*

In *E.* (*Archeoessigella*) (Fig. 1B), the dorsal major setae remain largely unchanged, although occasionally an anterad seta in either triangular set may be absent. The dorsal minors, however, usually increase in number over their expression in *Pseudessigella,* and several move posteromesally, coming nearer to the lateral-most dorsal majors. This has the effect of creating what superficially appears to be a band of setae in somewhat irregular positions across the tergum. There is, however, usually a retained association between at least one dorsal minor [the "lateral-most dorsal minor" in descriptions of species here] and the anterolaterad muscle attachment plate.

In *E.* (*Lambersella*), the next evolutionary step, two transitional expressions are found. In the more plesiomorphic arrangement (Fig. 1C), the dorsal majors remain intact, as do the dorsal minors, although the latter may be reduced in number. In the alternative state (Fig. 1D), among the dorsal majors, an anterad seta of either, or both, triangular set(s) may be lost; the dorsal minors may be reduced to two, and the most anterolaterad of these may or may not move posteriorly, away from its formerly associated position near the anterolaterad muscle attachment plate. This can result in the occasional occurrence of an individual (or population) with a series of only four dorsal (major + minor) setae occurring in a roughly straight line across the dorsum [a condition that mimics the first transition in *E.* (*Essigella*) mentioned below]; usually, however, when these setae are reduced to four, one of the laterad dorsal minors retains its anterolaterad position. These two expressions in *E.* (*Lambersella*) are not necessarily sequential, and either may occur within populations of any species of that subgenus.

Two expressions also occur within *E.* (*Essigella*), but these derived states are sequential. The first (Fig. 1E) typifies all *E.* (*Essigella*) with eight (or more) dorsals [i.e., *E.* (*E.*) *essigi, E.* (*E.*) *wilsoni, E.* (*E.*) *alyeska,* and the *E.* (*E.*) *knowltoni* complex]: the anterad seta of each dorsal major set is lost, leaving only two per set (four total). In very darkly pigmented specimens [e.g., *E.* (*E.*) *knowltoni knowltoni*] this is evident, under high magnification on slide mounted material, as a light spot that is the remnant location of the lost anterad dorsal major. The dorsal minors are also reduced to two on each side, and the lateral-most has moved back into a straight line with the remaining dorsal majors. The second expression (Fig. 1F) in *E.* (*Essigella*) occurs as only six (total) dorsals [i.e., *E.* (*E.*) *californica, E.* (*E.*) *hoerneri, E.* (*E.*) *pini*]. It is similar to that for the eight *E.* (*Essigella*) dorsals, except the dorsal minors are reduced to one on each side. Aberrations occur for

either of these expressions. In either the six or eight state, a suppressed dorsal major may reappear ahead of the line of setae in its normal anterad position. Also, in the eight setae state, one or more unsuppressed dorsal minors may occur, raising the setal count; these may involve a reversion to expression of the anterolaterad position.

The marginal setae are defined here as those setae laterad of the sagittally-oriented pair of muscle attachment points on the dorsum of each abdominal tergum (see Fig. 1; or Sorensen 1991: fig. 3). Like the dorsals, they are most easily seen on later nymphs. Among species, marginals may be expressed in a linear transformation, as states: four to six setae per side, three to five setae per side, or two setae per side. Their numbers are roughly correlated with the number of total dorsals. For example, E. (Archeoessigella) species, which have the most total dorsals, have four to six marginals per side; in contrast, those E. (Essigella) species with only six total dorsals have only two marginals per side. Marginal setal patterns show the greatest variation within species in more plesiomorphic states. The marginals of each side may occur in one or two groups, with the latter when their numbers are higher.

Setae on abdominal tergum VIII apparently have the same approximate transformation as the dorsals on segments III–IV. They vary among species in a linear transformation, from: 10–16 setae in two rows; to 8–12 setae in one or two rows; to 6, or occasionally 8 (rarely to 10), setae in one or occasionally two rows.

Dorsal Setae on the Metatibiae. — These setae often show considerable inter- and intraspecific variation in *Essigella.* In a principal component analysis of all *Essigella* taxa (Sorensen 1983), the length of dorsal setae on the metatibia, along with all other setae, show variation that is subordinate to general-size (component 1) and the number of abdominal setae (component 2). Tentatively, the dorsal setae of the metatibia are considered taxonomically useful only for apterous morphs. Their variation in *Essigella* contrasts with that of *Eulachnus* and other Lachninae, where their length appears to be more stable within species. This difference partially was responsible for the failure of previous attempts to circumscribe and key *Essigella* species (see Hottes 1957).

Hille Ris Lambers (unpublished notes), criticizing Hottes (1957), suggested "constant characters" within *Essigella* included "the length of tibial setae, but not their being blunt"; he also stated "in the same species more or fewer of the tibial setae may be blunt which accounts for a rather large variation in setal length in some species." I consider those statements to be erroneous. The retention of incrassate tips regardless of setal length, along with other characters, unifies the *E. (E.) knowltoni* group. Hottes (1957) erroneously defined his species on narrowly restricted setal length ranges; Hille Ris Lambers thought Hottes' use of setal length confused blunt versus sharp tipped setae, which although Hille Ris Lambers correctly viewed as a continuum, he unfortunately disregarded as being of any taxonomic value in *Essigella.* I have studied variation of the tip structure among the dorsal metatibial setae for *Essigella,* including scanning electron microscopy work, and recognize several degrees of expression of bluntness among tips (unpublished data); although of some taxonomic merit, this finer level delineation is not presented, because it cannot be used pragmatically to discriminate among most species.

Three aspects of the dorsal setae on the metatibiae are recognized and cate-

gorized here: (a) length dimorphism within individuals and species, (b) variability in the range of setal length within species, and (c) variability in the condition of setal tips within species. Only the characteristic patterns of expression of these setae are considered valid synapomorphies within *Essigella*. Generally, these setae are long in other Lachninae, and their length is obviously homoplasious within the subfamily. Because of potential confusion concerning reference to particular setae, only those setae on the central one-third of the metatibia are treated here; reference is usually to only the longest of dorsal setae for that section (generally the dorsal metatibial setae are shorter and more incrassate proximally, and longer and sharper distally).

The plesiomorphic state (state A) for dorsal setae of the metatibia within *Essigella* is short (ca. 0.3–0.7× tibial diameter) with incrassate tips; as in *Pseudessigella, E. (Archeoessigella)*, and *E. (E.) essigi*. From this plesiomorphic "short, incrassate" condition, three independent transformation series are hypothesized within *Essigella*. The first involves elongation of setae to a continuous length range of ca. 0.3–2.0+ × tibial diameter, with the tips of shorter setae incrassate and longer setae sharp. This intermediate state (state B) represents the normal relationship for setal length and tip expression in aphids. Transformation continues to an ultimate apomorphic state (state C) for this series, which shows an increase in the range of length variation to ca. 0.1–4.0+ × tibial diameter, and an increase in length variability within populations that I suspect is genetic and consider a weak synapomorphic character. This transformation is A → B → C.

The second independent transformation involves a single step elongation of the setae (state D) to a continuous length range of ca. 0.3–2.0+ × tibial diameter, but without the development of sharp tips. These setae are always incrassate, regardless of length, and are considered a valid synapomorphy for the *E. (E.) knowltoni* group. This transformation is: A → D.

The third independent transformation involves setal elongation, to a dimorphic length range spanning ca. 0.3–4.0+ × tibial diameter (state E). This dimorphism can occur as a discrete length difference among different individuals of a population, or may be expressed on single aphids as an abrupt change in setal length on the central part of the metatibiae; it is restricted to *E. (Lambersella)*, and appears to have ecological relevance between species of that subgenus in sympatry as a character displacement (unpublished data). Absence of the dimorphism in *E. (L.) hillerislambersi* may be a secondary loss for this accommodation. This transformation is A → E. Potentially confusing variation occurs in *E. (Essigella) californica*, where a minor increase in length of the dorsal setae is rarely evident on the distad one-third of the metatibiae; this is not considered homologous to the condition in *E. (Lambersella)*.

Ventral Abdominal Sclerites. —These sclerites represent attachment plates for muscles on the abdominal venter. Their size and shape may, therefore, have a functional relationship with the degree of sclerotization (not pigmentation) of the abdominal dorsum. Due to the diminished size and irregular variation of these ventral sclerites on more posterad abdominal segments, only segments III–IV are considered for taxonomic (identification) use. The sclerites are measured at their maximal length, along the anteroposterad axis, of the largest such sclerite occurring on abdominal segments III or IV. Unfortunately, the relative shapes and variance of these sclerites must be studied among species to be adequately comprehended.

As with the dorsal setae on the metatibiae, it is the qualitative pattern of expression of the ventral abdominal sclerites within populations, species, or species groups, that is considered taxonomically meaningful. In *Pseudessigella* (Sorensen 1991: figs. 2a–h), the ventral abdominal sclerites can be either uni-, bi-, or tripartite; if broken, the posterad section is relatively large and irregularly ovate, and the more anterad section(s) may be reduced and/or irregularly linear. In most species of less derived *Essigella*, these sclerites are subcircular to subquadrate [e.g., relative difference, Sorensen (1991: figs. 2e vs. 2f as bottom sclerite only of each, respectively)] (state A); this state occurs in *E.* (*Archeoessigella*), *E.* (*Lambersella*) and the more plesiomorphic species of *E.* (*Essigella*). To achieve this shape during evolution, it is unclear if a linear sclerite simply shortens, or if it breaks into multiple subsclerites and loses the more anteriad of these. Alternatively, in *E.* (*Lambersella*) these sclerites can be relatively linear [e.g., Sorensen (1991: figs. 2c–d)], which matches their most linear unbroken development in *Pseudessigella,* or they can be nearly absent; these alternative expressions are treated as state A here also.

Within *E.* (*Essigella*), several species show reduction of these sclerites, with expression varying from (at most) irregular, small quasi-stellate shapes through apparent absence (state B). This is considered homoplasious within the subgenus. Within the clade involving the *E.* (*E.*) *knowltoni* group, these sclerites ultimately become relatively enlarged and vary from subcircular or subquadrate to subelliptical [e.g., latter, Sorensen (1991: fig. 2a)] (state D); an intermediate expression (state C) exists for *E.* (*E.*) *alyeska,* however, in which the sclerites vary from between states B and D within populations. The transformation is considered to be A → B → C → D, but it could be independent among the latter three states.

Body Widths.—Body shape differences occur within the genus and primarily involve relative width. Width characters are usually unreliable on most slide mounted material, due to compression artifacts. The standardized mounting technique described earlier substantially reduces body distortion. Therefore, width measurements were used in analysis, but are avoided in keys and diagnoses, which must be applied to unstandardized slides.

Head width is measured between the most laterad rims of the bases of the antennal sockets. This anterad measurement minimizes the effects of compression that are more likely to occur posteriorly. It also enhances recognition of compression, because the measurement line is adjacent to the clypeal region and the anterad outline of the frons; distortion of these regions is relatively noticeable when they are compressed.

Relatively slight increases in width within species groups are homoplasious in this genus. Only the discrete and statistically significant broad body shown by the *E.* (*E.*) *knowltoni* group and *E.* (*E.*) *alyeska* is considered to be a valid synapomorphy. Although Moran (1986) warns against using such ecologically influenced traits, it is interesting that *E.* (*E.*) *hoerneri,* a relatively broad *Essigella* whose width correlates with its pinyon pine host's needle width, is correctly placed with *E.* (*E.*) *californica,* rather than the Series B *E.* (*Essigella*), in several discriminant function analyses (e.g., Sorensen 1992b: figs. 2a–b, 3) of the genus. This demonstrates the acceptable multivariate use of body width for classification (but not necessarily identification) within *Essigella.*

Lengths and Shapes of Appendage Segments.—Determination of the polarities

for transformations of antennal segment lengths in *Essigella* is difficult. The reduction from six to five antennal segments is a synapomorphy for *Essigella* and *Pseudessigella,* but is not unique in the Aphididae. In a principal component analysis among all *Essigella* taxa (Sorensen 1983), antennal segments III, IV and to a lesser extent V, load moderately on the second component. That vector orients largely to setal number on the abdominal dorsum, where polarity is clear. On the vector, however, the antennal segment lengths and abdominal setal numbers load in opposition; consequently, an increase in the relative length of antennal segments probably can be interpreted as apomorphic within the genus, as the abdominal setal number decline (Sorensen 1991, Sorensen & Foottit 1992).

Allometric variation in the length of the metatibiae, which is associated with different morphs and stages in *Essigella,* is confusing. Hottes (1957) and Hille Ris Lambers (unpublished notes) regarded relative tibial lengths as constant among species in the genus. In aphids generally, there is a tendency for alates, because of their generally longer legs, to have relatively longer metatibiae in comparison to body length than do adult viviparous apterae. The converse is often true of later stadia nymphs of viviparous apterae, which generally have relatively shorter metatibiae than do their apterous adults. Variation along this morph factor is discordant in *Essigella,* however. In some *E. (Archeoessigella)* and *E. (Essigella),* aberrant adult viviparous apterae exist that retain the relative metatibial length characteristic of the juvenile stages of their species. Several of Hottes' synonyms can be attributed to this aberrant variation among adult apterae [see the discussion of *E. (E.) californica*]. Contrastingly in *E. (Lambersella),* metatibial length is more stable within species; in that subgenus, however, allometric shifts along ontogenic factors, among species, sometimes differentiate the species in sympatry through character displacement.

The comparative length of metatarsal segments varies in *Essigella.* In *E. (Archeoessigella),* the metabasitarsus (first hind tarsus) is relatively short in regression compared to the metadistitarsus (second hind tarsus); a plesiomorphy reflected to a greater degree in *Pseudessigella.* Apomorphic elongation of the metabasitarsus occurs as a homoplasy in *E. (Essigella)* and *E. (Lambersella),* but reliable transformation of this homoplasious bivariate is difficult to ascertain; see Sorensen (1991) for a discussion of this trait.

In lateral view, the shape of the profemur of more primitive *Essigella* resembles that of *Pseudessigella.* In the latter, the dorsoproximal base of the femur is strongly swollen and arched. A similar, but less pronounced, swelling is evident in species such as *E. (A.) kathleenae,* and *E. (E.) pini,* among others. In most *Essigella,* however, the femur usually assumes a more cylindrical shape with elongation in response to increases in body size in various lineages, no doubt as a allometric size transformation. This trait is not employed in identification or phylogenetic assessments, because its variation is inadequately known and is difficult to characterize; it cannot be measured satisfactorily on slides because it is usually oriented in the dorsoventral axis.

Rostral Characters. —The rostrum of *Essigella* is retractile; consequently, rostral length is measured as the length of the stylets, which are fixed. Unfortunately, on slide mounted specimens the stylets can be withdrawn from the rostrum, and curved, making accurate measurement difficult. Stylets are measured from the sclerotic, basal apophyses in the clypeal region to their unbroken distal tips.

Essigella (E.) hoerneri shows the greatest apomorphic increase in stylet length in response to the exceptional needle fascicle width of its pinyon pine hosts. Measurement of the ultimate rostral segment includes the short, light-colored distal cap and the basal apophyses. Univariate or bivariate use of the ultimate rostral segment has not proven sufficiently reliable for consistent employment.

Caudal Protuberance. —Although Hottes (1957) used the median protuberance on the cauda as a diagnostic character, I have avoided this due to its variation and the potential for orientation artifacts on slides where the protuberance is obscured when the cauda points up. The caudal projection shows undoubtedly homoplasious reduction trends, but its transformation and polarity are confusing among species groups. *Essigella (E.) pini* shows the greatest development of the caudal protuberance, with the protrusion sometimes quite strongly pointed; this undoubtedly accounts for the use of the character as an ultimate, but problematic, diagnostic for that species in Hottes' (1957) key.

Nymphs. —In later stadia nymphs of viviparous apterae (not prealatae), a pair of bilateral sclerotized plates occur that surround the muscle attachment plates on the mesonotum; these may be large or small, depending upon the species. When large (e.g., their diameter approximates the length of the eye), the invasive sclerotizations of these plates extend from the muscle attachment sites to engulf neighboring setal bases. The mesonotal sclerotization on nymphs can be extremely faint, especially in the *E. (Archeoessigella)*, where the enlarged plates can be difficult to see because of their light pigmentation. This sclerotization probably has a similar history to that of the abdominal dorsum of adult viviparous apterae. Presence of the developed plates may be a synapomorphy unique to *Essigella* among the Eulachnina. The enlargement of these plates is treated as a plesiomorphy within the genus, however, and secondary losses of the plates are considered to be weak synapomorphies. In *E. (L.) fusca,* where the plates are normally enlarged, one late stadium nymph, within a large and otherwise normal sample, shows the loss of this invasive sclerotization. With this exception, the character appears quite stable among species; therefore, considering the loss state to be plesiomorphic on the basis of that single occurrence (i.e., a suppression failure) would require unacceptably strong homoplasy for the character. Nevertheless, the loss of these invasive sclerotizations, so that neighboring setal bases are free, appears to be a homoplasious apomorphy within *E. (Essigella)* for *E. (E.) californica, E. (E.) hoerneri, E. (E.) wilsoni* and *E. (E.) alyeska.*

Alatae. —*Essigella* alates are poorly known, and in several instances they are unknown. They appear to have few reliable diagnostic characters to identify them beyond species group. Characters often used within other genera, such as the number, shape or arrangement of secondary rhinaria on the antennae, usually show more intra- than interspecific variance in *Essigella.* Although *Essigella* alates normally have membranous abdominal terga, aberrants exist that show the normal sclerotic patterns of abdomens for their respective viviparous apterae or oviparae. Because knowledge of alate variation is poor, all statements concerning alate traits are tentative.

Although venation is often of quite questionable taxonomic use in aphids (V. Eastop, D. Hille Ris Lambers, personal communications), it may be used in *Essigella,* with great caution. For instance, in *Essigella* the medius may have one (or rarely two) furcation(s), or may be single. The furcation may arise on the

proximal, central or distal one-third of the vein. A single medius is most probably apomorphic; if so, then the only synapomorphy appears to be for E. (*E.*) *pini* and E. (*E.*) *essigi*. In both species, however, the vein can vary, uncommonly, to having a furcation on its distal one-third. Moreover, the medius is also rarely expressed as a single vein in aberrant alates of the E. (*E.*) *knowltoni* group; thus, polarity remains questionable.

Other variation of the medius involves the strength of expression of this entire vein system. Where the alates are known in E. (*Lambersella*), the medius is usually only faintly present along its entire length. This reduction is considered a weak synapomorphy. There are also differences involving the junctions of the anal and cubital veins with the radius. These can be expressed by the distance between the bases of the anal vein and the cubitus, along the radius, or by the truncated angle between them. The character is variable and tentatively considered unreliable as a diagnostic. An aberration displayed by several *Essigella* species is a darkened band that posteriorly parallels the radius.

The epicranial suture may be of use taxonomically. The suture appears to be most prominent and stable in E. (*E.*) *californica* and E. (*E.*) *hoerneri,* but varies in presence and expression among other species.

Oviparae. — Although the oviparae of all *Essigella* species are not known, among those that are, three conditions exist for the sclerotization/fusion of the abdominal dorsum: (state A) terga II–VII are fused, but I and VIII are free; (state B) abdominal terga II–VI are fused, but I, VII and VIII are free; and (state C) all abdominal terga are free with independently banded sclerotizations. It is unclear whether state A or B is the most plesiomorphic because both occur in E. (*Archeoessigella*); the transformation could be either A → B → C or A ← B → C. State A occurs in E. (*Archeoessigella*) *kathleenae,* in the E. (*Essigella*) *knowltoni* species-group, and usually in E. (*E.*) *pini*. State B occurs in E. (*Archeoessigella*) *kirki,* in E. (*Lambersella*), and rarely in E. (*E.*) *pini*. Therefore, the character is necessarily homoplasious, with state A either as a plesiomorphy, which requires a reversal in E. (*Essigella*), or as an apomorphy, which requires it to be gained independently in E. (*Archeoessigella*) and E. (*Essigella*). The complete loss of tergal fusion in state C, for the E. (*E.*) *californica* group, is considered a weak synapomorphy. Uncommon oviparae of species with the banded abdominal terga of state C can show near fusion of terga II–V or II–VI. This suggests an apparent plesiomorphic aberration approaching state B; if so, it appears C is apomorphic to B. No reversions from B or C to A are apparent; however, because E. (*E.*) *pini* usually shows fusion of abdominal terga II–VII, but with VI rarely free, this may be evidence for plesiomorphy in state B?

KEY TO THE EULACHNINA GENERA

1a. Antennae of adult virginoparous apterae 6-segmented. ....
   .... *Eulachnus* del Guercio
1b. Antennae of adult virginoparous apterae 5-segmented. 2
2a. (1b) Tarsal claws with single, simple tips. Adult apterae with tergum of
   abdominal segments II–VII membranous. ....
   .... *Pseudessigella* Hille Ris Lambers
2b. Tarsal claws incised, with double tips. Adult apterae with tergum of

abdominal segments II–VII fused, very lightly to heavily sclerotized.
. . . . *Essigella* del Guercio

ESSIGELLA DEL GUERCIO, 1909

Essigella Del Guercio, 1909, Riv. patol. Veg., Padov, n.s. 3: 329.
Lachnus Burmeister, 1835 (in part), Hardbuch der Entomologie, Berlin, 2: 91 (genus attributed to Illiger); Essig, 1909, Pomona J. Entomol., 1: 1–4.

Type Species. — *Lachnus californicus* Essig, 1909, Pomona J. Entomol., 1: 1–4; by monotypy.

Viviparous Apterae. — Body elongate, linear to linear-ovate. Antennae 5-segmented; processus terminalis short; accessory rhinaria on terminal antennal segment proximad, not directly against primary rhinarium. Head wider than long, fused with pronotum, or nearly so. Eyes without distinct triommatidia. Rostrum retractile; last rostral segment short, blunt, tip nonfunctionally articulated (if at all), accessory setae absent. Meso- and metanota fused dorsally. Abdominal dorsum lightly to heavily sclerotic; tergum I usually free; terga II–VII fused; tergum VIII free, represented by single, entire sclerotized field not apparently formed from fused lateral sclerites associated with setal bases; pigmentation variable; dorsal setae on segments III–IV in 1 or 2 often irregular rows. Siphunculi represented as rimmed pores to short truncated cones, without setae, incorporated into dorsal sclerotic field of abdomen. Cauda rounded, frequently with short, rounded to pointed, median protuberance. Profemora cylindrical-tapering, to dorsoproximad base slightly swollen. Tarsal claws incised, bifid; dorsal tip blunt, ventral tip sometimes slightly projecting, blunt to sharper.
Other Morphs. — Known fundatrices and males lacking siphunculi. Known oviparae and males apterous. Known alatae with radial sector short, straight; forewing medius distinct to apparently absent, single or with 1 furcation.

Diagnosis. — See the key to the Eulachnina genera and apomorphies section below.
Taxonomic Placement. — *Essigella,* along with *Pseudessigella* Hille Ris Lambers, 1966, and *Eulachnus* Del Guercio, 1909, comprise the subtribe Eulachnina (Sorensen 1990) of the tribe Cinarini, subfamily Lachninae; the subtribe is considered highly derived within the subfamily. The immediate sister-group of *Essigella* is *Schizolachnus*; which Lampel & Burgener (1987) suggest placing, along with the three eulachnine genera, in a single tribe, the Schizolachnini. Sorensen (1990), however, places *Schizolachnus* in a separate subtribe, the Schizolachnina. For commentary on the taxonomic relationships of related genera, and previous tribal/subtribal assignments, see Sorensen (1990).
Distribution. — *Essigella* is the only native Nearctic representative within the subtribe Eulachnina, although it has recently been introduced into Europe, in France (Turpeau & Remaudiere 1990) and Spain (Seco Fernandez & Mier Durante 1992). The other eulachnines, *Pseudessigella* and *Eulachnus,* are native to the Palaearctic; the former is known only from a single collection in the Himalayas of Pakistan (Sorensen 1991), but the latter has been introduced to the Nearctic where it occurs largely on cultivated Old World pines.
Apomorphies. — The three Eulachnina genera share these synapomorphies: body form linear; triommatidia of compound eye undifferentiated; ultimate rostral segment short and blunt, tip nonfunctionally articulated (if at all); accessory setae on ultimate rostral segment absent; setae on siphunculi absent; primary rhinarium without chitinous ring border; and accessory rhinaria on terminal antennal seg-

ment proximad and not directly against primary rhinarium. *Essigella* and *Pseudessigella* share these synapomorphies: reduction from six to five antennal segments; and abdominal tergum VIII represented by a single, entire sclerotized field that is not apparently formed from fused lateral sclerites that are associated with the dorsal setae bases.

Essigella is the most derived genus of the subtribe (Sorensen 1990) and has these autapomorphies: tarsal claws bifid; entire dorsum sclerotized; head and pronotum fused; meso- and metanotum fused dorsally; abdominal tergum I usually free (but at least partially fused [laterally] to metanotum as an autapomorphy in one species); abdominal terga II–VII fused. Another tentative autapomorphy for *Essigella* is a complete loss of the siphunculi in both the fundatrix and male, where these morphs are known; they are yet unknown for *Pseudessigella* and, therefore, the trait could be synapomorphic at that level. All *Essigella* have definitely incised tarsal claws, with the resultant presence of an endodontal lobe, despite Hottes' (1957) comments to the contrary; Hille Ris Lambers (personal communication, unpublished data) correctly interpreted Hottes' (1957: 108, key couplet 1a) statement of "Tarsal claws with ends not distinctly bifurcated" as erroneous, and due to over-processing in caustics during slide preparation.

Subgenera. — Three *Essigella* subgenera are recognized and described here; see the phylogenetics section for commentary. Their compelling separation requires discriminant function analysis of morphometric traits because considerable overlap in univariate traits exists among *Essigella* species (Sorensen 1983). Demarcation of these subgenera was made from an evolutionary perspective (see Sorensen 1992b) that includes *Pseudessigella* as an anagenic distance reference. Because many other aphid subgenera can be distinguished by single characters, their differentiation may be under the control of a single, or fairly limited number of, genes. As a result, such univariately defined subgenera probably display less genetic divergence than do the *Essigella* subgenera, among which realignments have occurred for large suites of genes (Falconer 1981, Sorensen 1991, Sorensen & Foottit 1992) that are responsible for their multivariate divergence. See Sorensen (1991) for a discussion of the multivariate evolution of the shape component among traits between *Pseudessigella* and *Essigella,* and among some *Essigella* groupings.

The phylogeny for the genus indicates *Archeoessigella,* the least derived subgenus, is separated (as Fig. 13: node 1) from *Pseudessigella* by 18.9 σ units (see phylogenetics section). *Lambersella* is separated from *Archeoessigella* by 2.08 σ units (as Fig. 13: internode 2–3). *Essigella* (*Essigella*), the most derived subgenus, is separated from *Lambersella* by 4.22 σ units (as Fig. 13: internode 3–7). All three of these anagenic distances are significant, at $\alpha = 0.05$, as evolutionary gaps between genus-[or subgenus]-level species assemblages (see phylogenetics section). Also, all three subgenera are phylogenetically convex (sensu Duncan 1980, Estabrook 1986), with *Lambersella* and *E.* (*Essigella*) as monophyletic groups.

Although the *Essigella* subgenera are quite valid biologically and evolutionarily, and their status as subgenera gives them the same nomenclatural rights as genera, they are described here with relevance *only for intrageneric hierarchy.* Because the anagenic distances among the *Essigella* subgenera are considerably shorter than among the genera in the Eulachnina, I recommend that these subgenera never be elevated to the status of full genera through taxonomic inflation.

Etymology. — The genus was named by Del Guercio (1909) after E. O. Essig, who collected and described its first species as *Lachnus californicus* Essig.

Material Examined. — All taxa proposed here, plus all Eulachnina and Schizolachnina taxa listed in Sorensen (1990: in Phylogenetic Construction sections Ingroup Material Examined and Outgroup Selection).

KEY TO THE SUBGENERA OF *ESSIGELLA*

This key is intended only for properly cleared, slide-mounted virginoparous apterae, and is meant for *populations and species, rather than individuals.* Key intraspecific samples with several (preferably $n = 10+$) individuals to account for variance. Individuals should be keyed using the key to *Essigella* species.

1a. Abdominal terga III–IV with dorsal setae in a single [or at most a very slightly staggered] row; lateral-most seta normally absent. Populational mean for number of dorsal setae on abdominal terga III–IV normally 6 or 8, mean number on abdominal tergum VIII normally 6, sometimes 8, never 9 or more [*if* mean on terga III–IV is 8–10 *and* the mean for tergum VIII is 8, *then*: (a) developed pigmentation suite for tibiae described in couplet 2a (below) never occurs in any population; *and* (b) populational mean for the ratio of length of the metadistitarsus to metabasitarsus is 1.73:1 or less; *and either* (c_1) body relatively broad with at least some populations with specimens whose longest dorsal setae on the central one-third of the metatibiae exceed $1.5\times$ metatibial diameter and remain incrassate regardless of length; *or* (c_2) metanotum and abdominal tergum I fused at least laterally; *or* (c_3) mesonotum of later stadia nymphs of apterae with area immediately surrounding muscle attachment sites membranous and bases of neighboring setae not on a sclerotized plate contiguous with the muscle attachment sites; *or* (c_4) mean number of marginal setae per side on each of abdominal terga III–IV is 2; *or* (c_5) primary rhinarium on terminal antennal segment exceptionally distad with distance from tip of processus terminalis to distal face of rhinarial rim less than $0.5\times$ diameter of rhinarium, and distal face of rhinarial rim usually perpendicular to longitudinal axis of antennal segment, and rhinarial membrane usually conspicuously protuberant]. . . . . *Essigella* (*Essigella*) del Guercio

1b. Abdominal terga III–IV with dorsal setae in a double [or strongly staggered] row; lateral-most seta normally present. Populational means for number of dorsal setae on abdominal terga III–IV and tergum VIII normally at least 8 or more, never 6 [*if* means on terga III–IV *and* tergum VIII are 8–10, *then either*: (a) any developed pigmentation suite described in couplet 2a (below) may or may not occur in any population; *or* (b) populational mean for the ratio of length of the metadistitarsus to metabasitarsus is 1.70:1 or greater; *but* (c) none of conditions c_1–c_5 in couplet 1a ever exist]. 2

2a. (2a) Populational mean for the ratio of length of the metadistitarsus to metabasitarsus is 1.69:1 or less, but usually under 1.65:1. Intraspecific pigmentation suites ranging from pale (unpigmented) to heavily pigmented, often within populations, but if developed (even subtly) then

(a) pro-, meso- and metatibiae, respectively, pigmented relatively heavily, lightly and heavily [in a dark-light-dark pattern], *or* (b) body dorsum with darkened pigmentation but with lightened longitudinal stripe in dorsomedial region of thorax and abdomen, *or* (c) thoracic and abdominal terga mottled with dorsal setal bases pigmented. In any population, longest dorsal seta on central one-third of metatibia varying from incrassate and short to long and either sharp or blunt tipped, but if longer than 1.0× metatibial diameter then they are not incrassate. Populational means for number of dorsal setae: (a) on each of abdominal terga III–IV usually 10 or less [occasionaly 11], but if mean more than 10 then at least some individuals with 9 or less; *and* (b) on abdominal tergum VIII usually 9 or less [occasionally 10], but if mean more than 9 then at least some individuals with 9 or less. . . . .
. . . . *Essigella* (*Lambersella*) NEW SUBGENUS

2b. Populational mean for the ratio of length of the metadistitarsus to metabasitarsus is 1.70:1 or greater, but usually over 1.75:1. Intraspecific pigmentation suites ranging from pale (unpigmented) to very subtly pigmented, but when pigmentation is subtly developed it is generally even and never as in couplet 2a. In any population, longest dorsal seta on central one-third of metatibia always incrassate and less than 1.0× metatibial diameter. Populational means for number of dorsal setae: (a) on each of abdominal terga III–IV usually 11 or more, but if mean less than 11 then at least some individuals with 13 or more; *and* (b) on abdominal tergum VIII usually 10 or more, but if mean less than 10 then at least some individuals with 12 or more. . . . .
. . . .*Essigella* (*Archeoessigella*) NEW SUBGENUS

ESSIGELLA (*ARCHEOESSIGELLA*), NEW SUBGENUS

"*Essigella* (*Archoessigella*)" Sorensen, 1983: 58 (unpublished manuscript name, note different spelling) Ph.D. Thesis, University of California at Berkeley, Berkeley, California. 605 p.

Type Species.—Essigella kathleenae Sorensen, 1988.

Viviparous Apterae.—Morphology: Body slender. Meso- and metanota fused dorsally; abdominal tergum I free. Dorsal setae (majors and minors) between muscle attachment plates on abdominal segments III–IV in 2 often irregular rows (see Fig. 1B); lateral-most minor dorsal setae on each side anterad (rarely not) of its immediately mesad neighbor. Abdominal terga III–IV each with 10–16 dorsal (major + minor) and 4–6 (per side) marginal setae; tergum VIII with 10–14, rarely 7–9, setae. Longest dorsal seta on central one-third of metatibiae less than tibial diameter, tips incrassate; these setae of nearly equal length along metatibiae, not dimorphic. Ventral abdominal sclerites on segments III–IV large, subquadrate or subcircular, not rudimentary. Species means for length ratio of metadistitarsus to metabasitarsus varying between 1.81:1 to 2.05:1. *Pigmentation:* Body dorsum unicolorously pale; bases of dorsal setae of abdomen concolorous with surrounding terga. All tibiae equally pigmented, usually pale to rarely subtly dusky.

Diagnosis. —See the key to the subgenera of *Essigella.*

Discussion. —This plesiomorphic subgenus is paraphyletic, but convex (sensu Duncan 1980, Estabrook 1986); no qualitative synapomorphies exist that uniquely define the group. It characteristically has a high ratio for the metabasitarsus:

metadistitarsus length, relatively many dorsal and marginal setae on abdominal terga III–IV and VIII, metatibial dorsal setae that are short and incrassate, no developed pigmentation suites, and species that are functionally monophagous and restricted to pine species in *Pinus* (*Strobus*), section Strobus, subsection Strobi. Except for some minor differences in placements of certain dorsal setae on the abdominal terga III–IV, intriguingly, all these characteristics are shared by *Pseudessigella* to a great degree. *Archeoessigella* was named because it differs significantly from *Lambersella* in several respects, and the two each have distinctly different host associations.

Similarities between the *Archeoessigella* species are relative plesiomorphies. The phylogenetic tree (Fig. 13), based on all 15 available dimensions of discriminant space, shows *E.* (*A.*) *kirki* to branch from node 1 (distance = 0) as the most primitive *Essigella*. However, when the multivariate shape-component differences for traits between *Essigella* and *Pseudessigella* were analyzed on the more dominant shape vectors, Sorensen (1991) found *E.* (*A.*) *kathleenae* to be generally more similar to *Pseudessigella* than to the remaining more derived *Essigella,* and he found *E.* (*A.*) *kirki* to be intermediate between those groups; he noted each *Archeoessigella* species was less similar to one another than either was to *Pseudessigella* or to the more derived *Essigella.* The closer proximity between *Pseudessigella* and *E.* (*A.*) *kathleenae* is also reflected on the second-most dominant minimum selective mortality vector (Fig. 14: DF2). A single, conventional, qualitative trait, the fusion of the abdominal dorsum in oviparae, sheds only vague light on the problem because its transformation and polarity are uncertain [see oviparae under the character discussion section].

Coded References to this Taxon.—Sorensen (1983) referred to this taxon under the manuscript name "*Essigella* (*Archoessigella*)." Sorensen (1987a) referred to the assemblage that comprise this taxon as group "I" or, with reference to its subcomponents, as "J–K"; in Sorensen (1992b), the latter refers to it.

Etymology.—"Archeo-" (Greek) = ancient; the name reflects the old and primitive status of the subgenus; coincidentally, the compounded name includes "-eoessig-" for E. O. Essig.

Material Examined.—*Essigella* (*A.*) *kathleenae, E.* (*A.*) *kirki.*

Essigella (*Archeoessigella*) *kirki* Sorensen,1988

Essigella kirki Sorensen, 1988: 121, Pan-Pacif. Entomol., 64: 121–124.
Essigella "*hottesi*" Sorensen, 1983: 60 (unpublished manuscript name) Ph.D. Thesis, University of California at Berkeley, Berkeley, California. 605 p.

Type Series.—Holotype. vivip. apt.; on slide with 3 paratype vivip. apt., holotype at lower left (8 o'clock position); data: NEW MEXICO. *SANTA FE Co.:* ca. 30 km NE of Santa Fe, hwy 475, 3100 m, 10 Aug 1978, J. T. Sorensen (78H55), *Pinus flexilis* James. Holotype retained in Sorensen collection, eventually to be deposited in The Natural History Museum, London. Paratypes (all same data as holotype): 19 vivip. apt. on 5 slides including holotype slide. Paratype slides deposited: 1 slide in NMNH, Washington, D.C.; 1 slide in CNC, Ottawa, Ontario; 2 slides in Sorensen collection.

Viviparous Apterae.—Morphology: Body length: 1.73–2.13 (1.92 ± 0.13) mm. HEAD: Primary rhinarium on terminal antennal segment (V) not exceptionally distad, distance from tip of processus terminalis to distal face of rhinarial rim greater than 0.5× diameter of rhinarium; distal face of rhinarial rim usually oblique to longitudinal axis of antennal segment; rhinarial membrane not conspicuously protuberant. Length of antennal segment V: 95–133 (117 ± 10) μ, processus terminalis: 28–45 (37 ± 5) μ; IV: 70–91 (82 ± 7) μ; III: 141–188 (157 ± 15) μ; II: 63–73 (68 ± 3) μ. Length of longest setae on frons: 10–43 (28 ± 9) μ, tips incrassate. Head width: 245–316 (285 ± 19) μ. Length of stylets: 530–694 (608 ± 55) μ; ultimate rostral segment: 68–83 (76 ± 5) μ, rostral tip reaching abdominal terga I or II in dorsal view through slide-mounted specimens. Head + pronotum fused, total length: 367–439 (399 ± 24) μ. THORAX: Meso + metanota fused, total length: 296–388 (347 ± 28) μ. ABDOMEN: Tergum I free, length: 112–163 (138 ± 15) μ; terga II–VII fused, VIII free. Maximum distal width of flange on siphunculi: 45–55 (50 ± 4) μ; siphunculi nearly flush to truncated conical, protruding to 1.0× maximal distal width. Ventral abdominal sclerites on segments III–IV subquadrate, subcircular to subelliptical; length: 50–68 (59 ± 6) μ, 1.2–2.0× diameter of metatibiae. Dorsal (major + minor) setae (see Fig. 1B) on abdominal terga III–IV: 10–14 (11 ± 1), tips sharp, in 2 irregular rows, lateral-most minor dorsal seta usually in anterad row; marginal setae 4–6 per segment each side. Setae on abdominal tergum VIII: 10–14 (11 ± 1), length: 5–43 (23 ± 11) μ, tips incrassate to rarely sharp, in 2 irregular rows. Cauda rounded; caudal protuberance moderately developed to frequently nearly absent; length of longest caudal setae: 70–103 (86 ± 10) μ, tips sharp. LEGS: Length of metafemora: 500–663 (578 ± 53) μ; metatibiae: 622–900 (755 ± 70) μ; longest dorsal setae on central one-third of metatibiae: 20–30 (24 ± 3) μ, 0.1–0.6× diameter of metatibiae, tips incrassate, approximately equal or very gradually increasing distally, no setal length dimorphism; longest ventral setae on metatibiae: 13–28 (23 ± 4) μ, tips sharp. Length of metabasitarsus: 93–118 (104 ± 7) μ; metadistitarsus: 165–213 (188 ± 13) μ. Ratio of metadistitarsus to metabasitarsus averaging 1.81:1, usually less than 1.9:1, rarely reaching 2.0:1 or slightly more. *Pigmentation:* Color in life: Gray-green, occasionally pale yellow throughout. Slide-mounted specimens: Background of body dorsum pale (to 10 percent pigment density), unicolorous. Terga at bases of setae on frons and dorsal (major + minor) setae on abdomen concolorous with surrounding terga. Thoracic muscle attachment plates pale, inconspicuous to conspicuous. Dorsal muscle attachment plates of abdomen conspicuous, pale, infrequently dusky. Spiracular plates and ventral abdominal sclerites usually light brown, slightly darker than background of abdominal terga, to pale. Siphunculi concolorous with surrounding terga. Cauda, anal and subgenital plates concolorous with abdominal terga. Antennal segments V and IV slightly to moderately dusky over entire segment, to moderately brown distally; III pale; II and I concolorous with frons. Pro-, meso- and metatibiae usually pale, concolorous, equivalent to body dorsum; frequently tibiae subtly dusky at distal tip, rarely entire tibiae moderately dusky, slightly darker than body dorsum. Distitarsi usually subtly dusky distally to moderate brown, varying with antennae, infrequently entirely dusky with tibiae.

Ultimate Stadium Nymphs of Viviparous Apterae.—Slide-mounted specimens: Nonmorphometrics as described for viviparous apterae except lacking body dorsum pigmentation suite; abdominal terga membranous with dorsal (major + minor) setae, between muscle attachment plates, arising from distinct scleroites. Mesonotum with 2 sclerotized plates extending from muscle attachment sites to engulf neighboring setal bases; plates usually vague, faintly pigmented, diameter approximately equaling eye length.

Oviparae.—Slide-mounted specimens: Nonmorphometrics as described for viviparous apterae except abdominal terga II–VI fused, lightly to moderately sclerotic, including pleural areas, but VII and VII free; dorsal demarcations of anterad terga not evident; siphunculi usually incorporated into sclerotic dorsum, to free; dorsal abdominal muscle attachment plates pale, unicolorous, except those between terga VI–VII darker. Pseudorhinaria on metatibiae irregular, difficult to distinguish, 7–11.

Viviparous Alatae, Males, Fundatrices.—Unknown.

Diagnosis.—Essigella (*A.*) *kirki* can easily be confused with other pale individuals of *Essigella*. It can be separated from all *Essigella*, except *E.* (*A.*) *kathleenae*, *E.* (*L.*) *eastopi*, *E.* (*L.*) *fusca*, *E.* (*L.*) *hillerislambersi*, and odd specimens of *E.* (*E.*) *wilsoni* and *E.* (*E.*) *knowltoni braggi*, by having 10 or more dorsal (major + minor) setae on abdominal terga III–IV, in two rows, with the lateral-most minor dorsal seta in the anterad row (e.g., Fig. 1B). *Essigella* (*A.*) *kirki* lacks the very
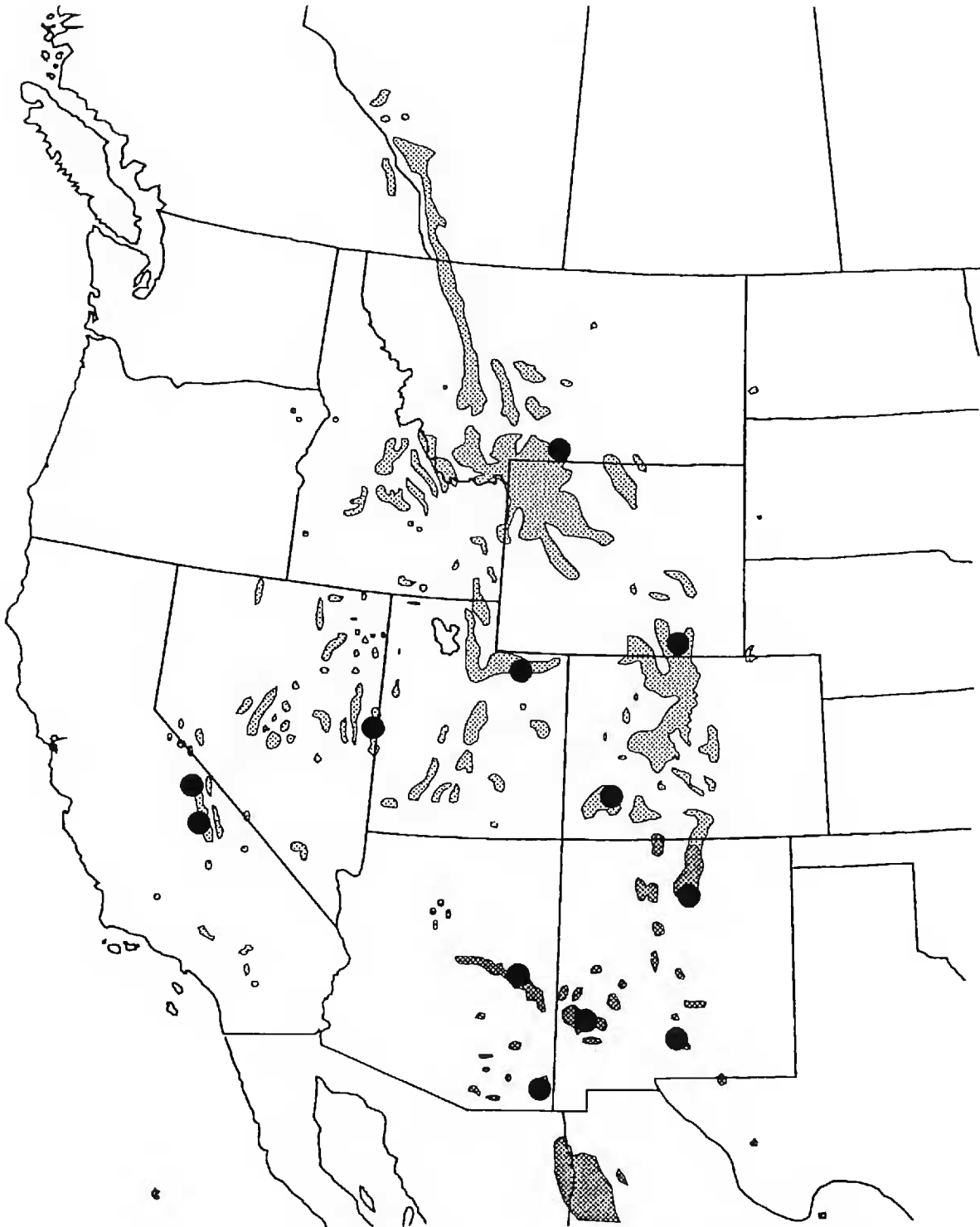
Figure 2. Distribution of *E. (A.) kirki* [dots (JTS samples)], superimposed over the ranges of its hosts, *Pinus flexilis* [lighter shading] and *Pinus strobiformis* [darker shading (AZ, NM and south)].

elongate metadistitarsus of *E. (A.) kathleenae,* having a metadistitarsus to meta-basitarsus ratio of usually less than 1.9:1, but rarely to 2.0:1 [mean: 1.8:1 for *E. (A.) kirki,* 2.05:1 for *E. (A.) kathleenae*]. It can be separated from other pale *Essigella,* however, by having this ratio at over 1.7:1. *Essigella (A.) kirki* lacks the protuberant, exceptionally distad primary rhinarium of *E. (E.) wilsoni.* It can be further distinguished from pale *E. (L.) fusca* and *E. (L.) hillerislambersi,* and some pale *E. (L.) eastopi* and *E. (E.) knowltoni braggi* by having the longest dorsal setae on the central part of the mesotibia less than 0.7× tibial diameter. All observed *E. (E.) knowltoni braggi* with 10 or more dorsal (major + minor) setae on abdominal terga III–IV differ from *E. (A.) kirki* by having the longest dorsal metatibial setae in excess of 1.0× tibial diameter; however, rare, confusing *E. (E.) knowltoni braggi* are anticipated, and these could be separated by their broad

head on noncompressed slides, and by usually longer setae on the frons [see descriptions and *E.* (*E.*) *knowltoni* diagnosis].

Range.—Rocky Mountains, Montana to Arizona and New Mexico; southern Sierra Nevada (east slope) and White Mountains of California; presumably into Mexico and Canada with its hosts (Fig. 2).

Hosts.—*Pinus flexilis* James and *P. strobiformis* Engelmann; the latter was previously considered to be a variety [as *P. flexilis* var. *reflexa* Engelmann] of the former. These pines split the higher elevation niche in the Rocky Mountains, with *P. flexilis* in the north, *P. strobiformis* in the south, and some intergradation at their contact in northern New Mexico (Critchfield & Little 1966). The only other *Essigella* species on these pines is *E.* (*E.*) *californica,* which has secondarily invaded the niche, opportunistically, and is much less common in it than *E.* (*A.*) *kirki.*

It is possible that *E.* (*A.*) *kirki* also occurs on *P. ayacahuite* Ehrenberg in central Mexico and south, because that pine was formerly considered a variety of *P. strobiformis* (as *P. ayacahuite* var. *brachyptera* Shaw); *P. ayacahuite* apparently continues the *P. flexilis* to *P. strobiformis* morphological and geographic cline (Critchfield & Little 1966), and although discontinuous with the latter, a single isolated stand in western Jalisco, Mexico (Critchfield & Little 1966: map 9) is morphologically intermediate with *P. strobiformis* (Martínez 1948).

Discussion.—Because of previous misinterpretation of meso- and metanotal fusion in *Essigella* (see character discussion section), the description given here for this species is more accurate than that in Sorensen (1988).

Essigella (*A.*) *kirki* is a common species that is relatively homogeneous, morphologically, and always pale, unlike several other *Essigella* species that can grade from pale to fully pigmented; in these respects it resembles *E.* (*A.*) *kathleenae.* Sorensen (1983) determined that it differs from the latter in bivariate plots of head width, between the lateral rims of the antennal sockets, versus body length, and of metadistitarsus versus metabasitarsus lengths; it also separates under principal component and discriminant function analyses (Sorensen 1983).

Coded References to This Taxon.—*Essigella* (*A.*) *kirki* has been referred to previously by: the coding "Sp. K" (Sorensen 1983, 1987a, 1992b) and "HOTT" (Sorensen 1983), and by the manuscript name *E.* "*hottesi*" in Sorensen (1983).

Etymology and Common Name.—The species was named for my son, Kirk Hale Sorensen. Common name: Kirk's limber pine needle aphid.

Material Examined.—ARIZONA. *APACHE Co.:* Lake Harney Rd (hwy 473), nr McNary, 2440 m, 11 Sep 1978, JTS 78I14, *P. strobiformis,* (apt.). *COCHISE Co.:* nr Rustler Park, Chiricahua Mts, 2500 m, 16 Sep 1978, JTS 78I50, *P. strobiformis,* (apt.). CALIFORNIA. *INYO Co.:* Lake Sabrina, nr Bishop, 2750 m, 1 Aug 1977, JTS 77H2, *P. flexilis,* (apt.); Onion Valley Cmpgd, 24 km W of Independence, 2770 m, 4 Aug 1978, JTS 78H13, *P. flexilis,* (apt.). COLORADO. *SAN JUAN Co.:* 20 km N of Purgatory, 3020 m, 8 Aug 1978, JTS 78H47, *P. flexilis,* (apt.). MONTANA. *CARBON Co.:* Red Lodge, 1770 m, 20 Aug 1978, JTS 78H115, *P. flexilis,* (apt.). NEVADA. *WHITE PINE Co.:* Wheeler Peak, 3140 m, 26 Aug 1978, JTS 78H147, *P. flexilis,* (apt., ovip.). NEW MEXICO. *OTERO Co.:* 3 km W of Cloudcroft on hwy 82, 2560 m, 13 Sep 1978, JTS 78I22, *P. strobiformis,* (apt., ovip.). *SANTA FE Co.:* (type series) 30 km NE of Santa Fe on hwy 475, 3100 m, 10 Aug 1978, JTS 78H55, *P. flexilis,* (apt.). *SIERRA Co.:* Emory Pass on hwy 90, W of Kingston, 2470 m, 14 Sep 1978, JTS 78I34, *P. strobiformis,* (apt.). UTAH. *DUCHESNE Co.:* 19 km NE of Castle Gate on hwy 33, 2770 m, 25 Aug 1978, JTS 78H144, *P. flexilis,* (apt.). WYOMING. *ALBANY Co.:* 5 km SW of Woods Landing on hwy 230, 2560 m, 15 Aug 1978, JTS 78H92, *P. flexilis,* (apt.).

Essigella (Archeoessigella) kathleenae Sorensen, 1988

Essigella kathleenae Sorensen, 1988: 115, Pan-Pacif. Entomol., 64: 115–118.
Essigella "kathleeni" Sorensen, 1988: 124 (lapsus), Pan-Pacif. Entomol., 64: 124.
Essigella "kathleenae" Sorensen, 1983: 67 (unpublished manuscript name) Ph.D.
   Thesis, University of California at Berkeley, Berkeley, California. 605 p.

Type Series. — Holotype, vivip. apt.; on slide with 3 paratype vivip. apt., holotype at upper left (11 o'clock position); data: CALIFORNIA. *SAN BERNARDINO Co.*: 3 km S of jct hwy 38 & Jenks Lake Rd, San Bernardino Mts, 2200 m, 16 Sep 1977, J. T. Sorensen (77I38), *Pinus lambertiana* Douglass. Holotype retained in Sorensen collection, eventually to be deposited in The Natural History Museum, London. Paratypes (all same data as holotype): 30 vivip. apt. on 7 slides including holotype slide. Paratype slides deposited: 1 slide in NMNH, Washington, D.C.; 1 slide in CNC, Ottawa, Ontario; 8 slides in Sorensen collection.

Viviparous Apterae. — *Morphology:* Body length: 1.35–2.01 (1.67 ± 0.18) mm. HEAD: Primary rhinarium on terminal antennal segment (V) not exceptionally distad, distance from tip of processus terminalis to distal face of rhinarial rim greater than 0.5× diameter of rhinarium; distal face of rhinarial rim usually oblique to longitudinal axis of antennal segment; rhinarial membrane not conspicuously protuberant. Length of antennal segment V: 85–113 (102 ± 7) μ, processus terminalis: 28–43 (40 ± 4) μ; IV: 60–90 (75 ± 9) μ; III: 98–135 (118 ± 11) μ; II: 55–68 (62 ± 4) μ. Length of longest setae on frons: 8–25 (17 ± 6) μ, tips incrassate. Head width: 215–258 (242 ± 11) μ. Length of stylets: 428–653 (581 ± 64) μ; ultimate rostral segment: 55–78 (66 ± 5) μ, rostral tip reaching metanotum to abdominal terga III in dorsal view through slide-mounted specimens. Head + pronotum fused, total length: 286–377 (334 ± 31) μ. THORAX: Meso + metanota fused, total length: 214–306 (280 ± 31) μ. ABDOMEN: Tergum I free, length: 93–133 (119 ± 12) μ; terga II–VII fused, VIII free. Maximum distal width of flange on siphunculi: 23–38 (32 ± 4) μ; siphunculi flush to truncated conical, protrusion to 0.5× maximum distal width. Ventral abdominal sclerites on segments III–IV subcircular, subquadrate to subelliptical; length: 36–60 (48 ± 8) μ, 1.3–2.1× diameter of metatibiae. Dorsal (major + minor) setae (see Fig. 1B) on abdominal terga III–IV: 11–14 (12 ± 1), tips sharp, in 2 irregular rows; marginal setae 4–5 per segment each side. Setae on abdominal tergum VIII: 7–13 (10 ± 2), length: 5–40 (14 ± 10) μ, tips incrassate to sharp, in 2 irregular rows. Cauda rounded; caudal protuberance moderately developed, to infrequently nearly absent; length of longest caudal setae: 40–93 (61 ± 16) μ, tips sharp. LEGS: Length of metafemora: 316–541 (448 ± 67) μ; metatibiae: 428–704 (569 ± 77) μ; longest dorsal setae on central one-third of metatibiae: 5–23 (13 ± 6) μ, 0.1–0.8× diameter of metatibiae, tips incrassate; approximately equal or very gradually increasing distally, no setal length dimorphism; longest ventral setae on metatibiae: 10–25 (19 ± 5) μ, tips sharp. Length of metabasitarsus: 60–95 (79 ± 10) μ; metadistitarsus: 135–180 (162 ± 12) μ. Ratio of metadistitarsus to metabasitarsus averaging 2.05:1, greater than 1.9:1, and usually greater than 2.0:1. *Pigmentation:* Color in life: Pale yellow throughout. Slide-mounted specimens: Background of body dorsum pale (usually to 10, sometimes to 30, percent pigment density), unicolorous. Terga at bases of setae on frons and dorsal (major + minor) setae on abdomen concolorous with surrounding terga. Thoracic muscle attachment plates and dorsal muscle attachment plates of abdomen, pale, inconspicuous. Spiracular plates and ventral abdominal sclerites pale. Siphunculi concolorous with surrounding terga. Cauda, anal and subgenital plates pale, concolorous with abdominal terga, to slightly darker. Antennal segments V and IV pale, only very subtly darker than body dorsum; III very pale to distal one-third pale as V and IV; II concolorous with proximal III; I concolorous with frons. Pro-, meso- and metatibiae usually pale, concolorous with body dorsum, to very subtly darker. Distitarsi entirely pale to subtly dusky on distal one-third.

Ultimate Stadium Nymphs of Viviparous Apterae. — Slide-mounted specimens: Nonmorphometrics as described for viviparous apterae except lacking body dorsum pigmentation suite; abdominal terga membranous with dorsal (major + minor) setae, between muscle attachment plates, arising from distinct scleroites. Mesonotum with 2 sclerotized plates extending from muscle attachment sites to engulf neighboring setal bases; plates usually vague, faintly pigmented, diameter approximately equaling eye length.

Oviparae.—Slide-mounted specimens: Nonmorphometrics as described for viviparous apterae, abdominal terga II–VII fused, lightly to moderately sclerotic, including pleural areas, tergum VIII free; dorsal demarcations of anterad terga not evident; siphunculi incorporated into sclerotic dorsum; dorsal abdominal muscle attachment plates pale, unicolorous. Pseudorhinaria on metatibiae irregular, difficult to distinguish, 5–9.

Viviparous Alatae, Males, Fundatrices.—Unknown.

Diagnosis.—*Essigella* (*A.*) *kathleenae* is consistently pale, and usually can be identified by the unique, exceptionally long metadistitarsus and short metabasitarsus. The length ratio of the metadistitarsus to metabasitarsus usually exceeds 2.0:1, and only rarely approaches 1.9:1, the upper value for all other *Essigella,* except occasional *E.* (*A.*) *kirki.*

Range.—California and southwestern Oregon (Fig. 3).

Hosts.—*Pinus lambertiana* Douglass; questionable single occurrences on *P. jeffreyi* Greville & Balfour, *P. sabiniana* Douglass and *P. monticola* Douglass. A single specimen attributed to *P. jeffreyi* (77I66) is probably a beating tray contamination from a preceding collection (77I64) from *P. lambertiana,* which occurred at dusk. A single specimen from *P. sabiniana* (77G17) is probably also similarly accidental, following a preceding collection on *P. lambertiana* (77G16). My collection from *P. monticola* (78G7) is a questionable host determination; that collection is from an isolated, low elevation stand of pines that W. B. Critchfield (personal communication) believes to be *P. monticola,* but that I believe is possibly *P. lambertiana* on the basis of its ecological, geographic and elevational circumstances [*P. monticola* replaces *P. lambertiana* at higher elevations in the Sierra Nevada, and the *P. monticola* niche is opportunistically occupied by *E.* (*E.*) *californica.*]

Discussion.—Because of previous misinterpretation of meso- and metanotal fusion in *Essigella* (see character discussion section), the description given here for this species is more accurate than that in Sorensen (1988).

Essigella (*A.*) *kathleenae* is a common, morphologically homogeneous species. Its elongate metadistitarsus and very shortened metabasitarsus represent a plesiomorphy within *Essigella*; this is shared with *Pseudessigella,* which has a much higher tarsal ratio and differing metatarsal regression. *Essigella* (*A.*) *kirki* nearly shares the same metatarsal regression with *E.* (*A.*) *kathleenae,* but is displaced along the regression by its slightly longer metabasitarsus. *Essigella* (*A.*) *kathleenae* may have no conventional apomorphies beyond those defining the genus; the confusing polarity for the fused abdominal terga of oviparae, which differs between *E.* (*A.*) *kathleenae* and *E.* (*A.*) *kirki,* is discussed in the character discussion section.

Coded References to This Taxon.—*Essigella* (*A.*) *kathleenae* has been referred to previously by: the coding "Sp. J" (Sorensen 1983, 1987a, 1992b) and "KATH" (Sorensen 1983), and by the manuscript name *E.* "*kathleenae*" in Sorensen (1983).

Etymology and Common Name.—The species is named for my wife, Kathleen Hale Sorensen, who served as my field botanist during this study. Common name: Kathleen's sugar pine needle aphid.

Material Examined.—CALIFORNIA. *CALAVERAS Co.:* 18 km E of Arnold on hwy 4, 1680 m, 17 Jul 1977, JTS 77G45, *P. lambertiana,* (apt.). *DEL NORTE Co.:* Panther Flat Cmpgd, Six Rivers Natl Forest, at Pioneer Rd & hwy 199, E of Gasquet, 4 Jul 1978, JTS 78G7, *P. monticola,* (apt.). *EL DORADO Co.:* Lake Tahoe, Emerald Bay, 1980 m, 16 Jul 1977, JTS 77G30, *P. lambertiana,* (apt.). *FRESNO Co.:* jct of hwy 180 & Sequoia Lake turnoff, nr Pinehurst, 1710 m, 13 Aug 1977, JTS
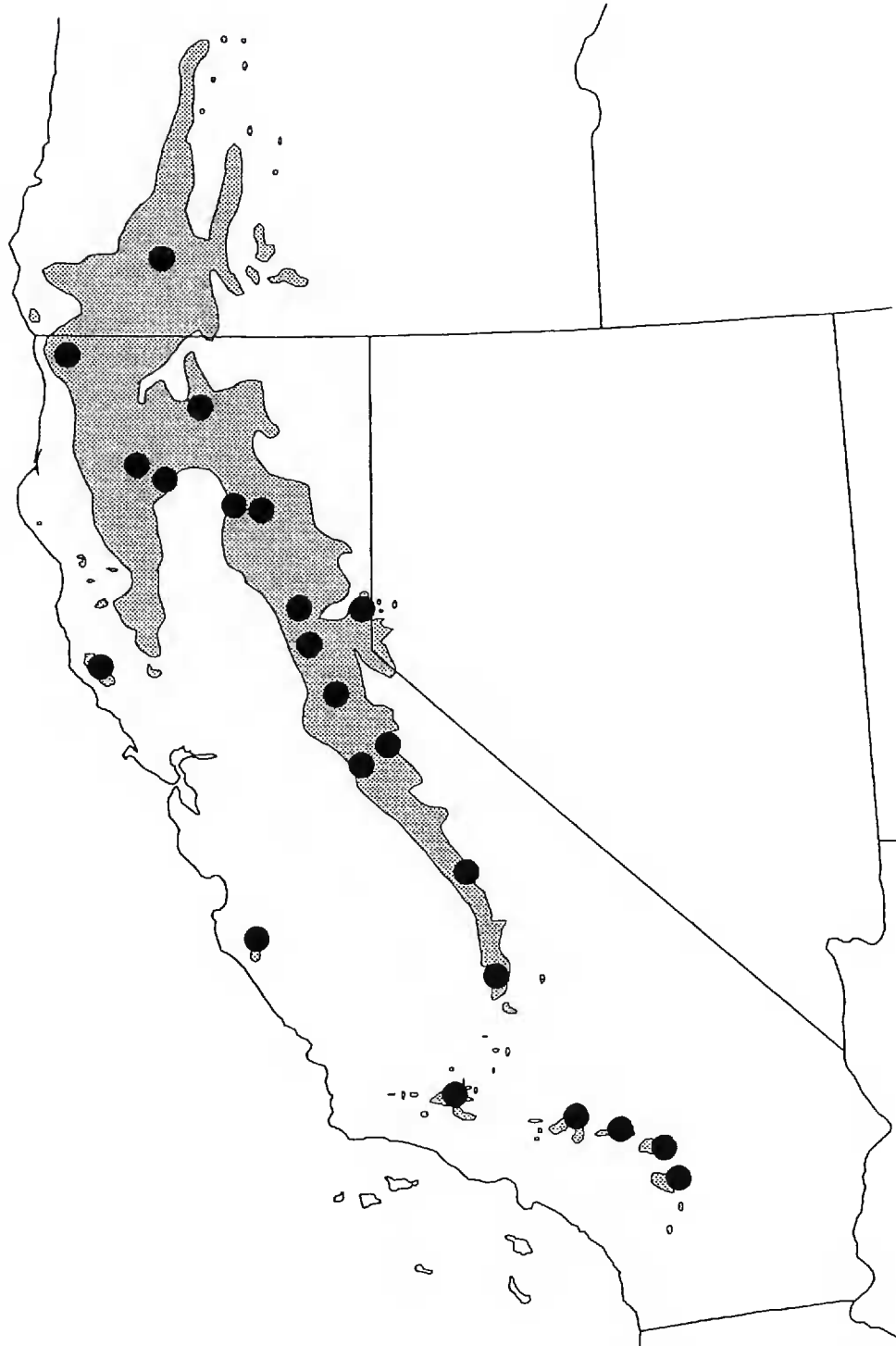
Figure 3. Distribution of *E. (A.) kathleenae* [dots (JTS samples)], superimposed over the range of its host, *Pinus lambertiana* [shaded].

77H10, *P. lambertiana,* (apt.). *KERN Co.:* Tiger Flat Rd, N of hwy 155, nr Alta Sierra, 1890 m, 20 Sep 1977, JTS 77I64, *P. lambertiana,* (apt.); same but JTS 77I66, *P. jeffreyi,* (apt.). *LOS ANGELES Co.:* 3 km SE of Big Pines on hwy 2, E of Blue Ridge Summit, 2200 m, 17 Sep 1977, JTS 77I48, *P. lambertiana,* (apt., ovip.). *MARIPOSA Co.:* Yosemite Natl Park, 13 km W of Crane Flat on hwy 120, 2140 m, 1 Aug 1977, JTS 77H6, *P. lambertiana,* (apt.). *MENDOCINO Co.:* Fish Rock Rd, 27 km E of hwy 1, 490 m, 23 Jul 1977, JTS 77G49, *P. lambertiana,* (apt.). *MONTEREY Co.:* Cone Peak Rd, 13 km N of jct with Nacimento-Fergusson Rd, Los Pardes Natl Forest, 1310 m, 4 Sep 1977, JTS 77I10, *P. lambertiana,* (apt.). *PLACER Co.:* 5 km SW of Whitmore on hwy 80, 1430 m, 25 Jun 1977, JTS 77F2, *P. lambertiana,* (apt.). *PLUMAS Co.:* hwy 36, 6 km W of jct with hwy 89, 1460 m, 10 Jul 1977, JTS 77G22, *P. lambertiana,* (apt.); 8 km E of Chester on hwy 36, 1520 m, 4 Jul 1977, JTS 77G16, *P. lambertiana,* (apt.). *RIVERSIDE Co.:* South Ridge Rd, nr Idyllwild, 1770 m, 9 Sep 1977, JTS 77I21, *P. lambertiana,* (apt.). *SAN BERNARDINO Co.:* (type series) San Bernardino Mts, 3 km S of jct of hwy 38 & Jenks Lake Rd, 2200 m, 16 Sep 1977, JTS 77I38, *P. lambertiana,* (apt.); same but 3 km S of Lake Gregory, 1490 m, 17 Sep 1977, JTS 77I45, *P. lambertiana,* (apt.). *SISKIYOU Co.:* Mt Shasta Ski Bowl Rd, 2450 m, 2 Jul 1977, J. T. Sorensen & D. J. Voegtlin, JTS 77G8, *P. lambertiana,* (apt.). *TEHAMA Co.:* Lanes Valley Rd, nr jct with hwy 36, 490 m, 4 Jul 1977, JTS

77G17, *P. sabiniana,* (apt.). *TRINITY Co.:* East County Line Rd, 5 km S of Buckhorn Summit on hwy 299, W of Tower, 1530 m, 20 Aug 1977, JTS 77H19, *P. lambertiana,* (apt.). *TUOLUMNE Co.:* 2 km E of Groveville on hwy 120, 910 m, 30 Jul 1977, JTS 77G62, *P. lambertiana,* (apt.); same but JTS 77G63, *P. ponderosa,* (apt.). *VENTURA Co.:* Reyes Peak Rd, 10 km E of Pine Mt Summit on hwy 33, 2200 m, 19 Sep 1977, JTS 77I58, *P. lambertiana,* (apt.). OREGON. *JACKSON Co.:* 15 km S of Union Creek on hwy 62, 850 m, 5 Jul 1978, JTS 78G17, *P. lambertiana,* (apt.).

Essigella (*Lambersella*), NEW SUBGENUS

"*Essigella* (*Lambersella*)" Sorensen, 1983: 73 (unpublished manuscript name) Ph.D. Thesis, University of California at Berkeley, Berkeley, California. 605 p.

Type Species.—*Essigella fusca* Gillette & Palmer, 1924, Ann. Entomol. Soc. Am., 17: 6–9.

Viviparous Apterae.—*Morphology:* Body not relatively broad. Meso- and metanota fused dorsally; abdominal tergum I free. Dorsal setae (majors and minors) between muscle attachment plates on abdominal segments III–IV in 2 (rarely 1) often irregular rows (see Figs. 1C–D); lateral-most dorsal minor seta on each side anterad (rarely not) of its immediately mesad neighbor. Abdominal terga III–IV each with 8–12 dorsal (major + minor) and 3–5 (per side) marginal setae; tergum VIII with 8–11, rarely 12, setae. Longest dorsal seta on central one-third of metatibiae to nearly 4× tibial diameter, tips incrassate to sharp, sometimes reflexed; these setae sometimes dimorphic in length or with abrupt length transition, nearly doubling, centrally on the metatibiae. Ventral abdominal sclerites on segments III–IV reduced (rudimentary), irregular stellate to large, subquadrate to sublinear, often broken into linearly separated parts. Species means for length ratio of metadistitarsus to metabasitarsus varying between 1.39:1 to 1.54:1. *Pigmentation:* Body dorsum variable, pale to dark brown, background unicolorous or not, often mottled; bases of dorsal setae of abdomen concolorous with surrounding terga to substantially darker. Tibiae varying from entirely pale to nearly black, but when darkened mesotibiae at least subtly to usually substantially paler than pro- and metatibiae.

Diagnosis.—See the key to the subgenera of *Essigella.*

Discussion.—*Lambersella* is monophyletic and convex (sensu Duncan 1980, Estabrook 1986), and represents the sister clade of *E.* (*Essigella*). The major nonhomoplasious, qualitative synapomorphy for this subgenus is its "dark-light-dark" tibial pigmentation suite for the pro-, meso- and metatibiae, respectively. Also, unlike any other *Essigella,* there is also a tendency for the ventral abdominal sclerites on segments III–IV to often be linear; that trait is problematic, however, because it is shared by *Pseudessigella* (e.g., Sorensen 1991: figs. 2b–e). I consider a length dimorphism of the dorsal setae on the metatibiae [except *E.* (*L.*) *hilleris-lambersi*] and the usually faint, to absent, forewing medius of alates [morph unknown for *E.* (*L.*) *eastopi*] to be apomorphies that are unique to *Lambersella,* but that are not found in, or known from, all its species. Of the *Lambersella* species, the phylogenetic analysis (Fig. 13) shows *E.* (*L.*) *eastopi* to be the least derived (closest to the ancestral node 3) and *E.* (*L.*) *hillerislambersi* the most, in anagenic distance from node 3.

Ecologically, *Lambersella* has invaded the genetically distinct subsection Ponderosae of the diploxylon pines (subgenus *Pinus*); only *E.* (*L.*) *eastopi* feeds chiefly on a subsection Sabinianae pine, perhaps reflecting its relatively primitive status in the subgenus. Sorensen (1983: section 2) analyzed the relationships among the taxa within this subgenus; see the discussion under *E.* (*L.*) *eastopi* for a summary. An apparent case of character displacement has occurred under sympatry in California between *E.* (*L.*) *fusca voegtlini* and *E.* (*L.*) *hillerislambersi,* with respect to bivariant regressions of the length of dorsal setae on the metatibia versus metatibial length (unpublished data); see discussion of *E.* (*L.*) *fusca voegtlini.* This

suggests that *Lambersella* species compete for their pine hosts as resources, as apparently do species in the *E.* (*E.*) *knowltoni* group of *E.* (*Essigella*) (Sorensen 1992a), where a similar form of character displacement also occurs.

Coded References to This Taxon. —Sorensen (1983) referred to this taxon under the manuscript name "*Essigella* (*Lambersella*)." Sorensen (1987a) referred to the assemblage that comprises this taxon as group "II" or, with reference to its sub-components, as "O-N-M-L" [or *entire* permutations therefore]; in Sorensen (1992b), the latter refers to it.

Etymology. —The subgenus is named for Dirk Hille Ris Lambers, who pointed out the tibial pigmentation synapomorphy.

Material Examined. —*Essigella* (*L.*) *eastopi, E.* (*L.*) *fusca fusca, E.* (*L.*) *fusca voegtlini, E.* (*L.*) *hillerislambersi.*

Essigella (*Lambersella*) eastopi, NEW SPECIES

Essigella "eastopi" Sorensen, 1983: 76 (unpublished manuscript name) Ph.D. Thesis, University of California at Berkeley, Berkeley, California. 605 p.

Type Series. —Holotype, vivip. apt.; on slide with 1 paratype vivip. apt., holotype on top (12 o'clock position); data: CALIFORNIA. *SAN DIEGO Co.:* 8 km N of Mt Laguna, hwy S1, 1700 m, 12 Sep 1977, J. T. Sorensen (77I32), *Pinus coulteri* D. Don. Holotype deposited in The Natural History Museum, London. Paratypes (all same data as holotype): 17 vivip. apt. on 5 slides including holotype slide. Paratype slides deposited: 1 slide in NMNH, Washington, D.C.; 1 slide in CNC, Ottawa, Ontario; 2 slides in Sorensen collection. (The type series represents smaller, darker specimens with short setae; these are the more distinctive form of *E.* (*L.*) *eastopi.*)

Viviparous Apterae. —*Morphology:* Body length: 1.65–1.98 (1.84 ± 0.09) mm. HEAD: Primary rhinarium on terminal antennal segment (V) not exceptionally distad, distance from tip of processus terminalis to distal face of rhinarial rim greater than 0.5 × diameter of rhinarium; distal face of rhinarial rim usually oblique to longitudinal axis of antennal segment; rhinarial membrane not conspicuously protuberant. Length of antennal segment V: 105–133 (118 ± 8) μ, processus terminalis: 30–40 (34 ± 3) μ; IV: 73–88 (82 ± 5) μ; III: 133–183 (146 ± 13) μ; II: 65–73 (69 ± 2) μ. Length of longest setae on frons: 45–66 (52 ± 8) μ, tips incrassate to sharp. Head width: 270–306 (286 ± 11) μ. Length of stylets: 714–836 (766 ± 39) μ; ultimate rostral segment: 65–90 (81 ± 8) μ, rostral tip reaching abdominal terga I–III in dorsal view through slide-mounted specimens. Head + pronotum fused, total length: 357–428 (385 ± 21) μ. THORAX: Meso + metanota fused, total length: 316–388 (348 ± 21) μ. ABDOMEN: Tergum I free, length: 133–184 (158 ± 21) μ; terga II–VII fused, VIII free. Maximum distal width of flange on siphunculi: 33–45 (40 ± 3) μ; siphunculi truncated conical, protrusion 0.2– 0.6 × maximal distal width. Ventral abdominal sclerites on segments III–IV subquadrate, subelliptical to sublinear; length: 44–59 (52 ± 5) μ, 1.3–2.0× diameter of metatibiae. Dorsal (major + minor) setae (see Figs. 1C–D) on abdominal terga III–IV: 8–10 (9 ± 1), tips blunt to sharp, in 2 (rarely 1) rows with setae in regular positions, lateral-most minor dorsal seta in anterad row (rarely not); marginal setae 3–4 per segment each side. Setae on abdominal tergum VIII: 8–11 (9 ± 1), length: 45–73 (55 ± 9) μ, tips incrassate to sharp, in 1 or 2 irregular rows. Cauda rounded; caudal protuberance absent to poorly developed; length of longest caudal setae: 75–103 (91 ± 9) μ, tips sharp. LEGS: Length of metafemora: 490–704 (578 ± 59) μ; metatibiae: 612–908 (699 ± 84) μ; longest dorsal setae on central one-third of metatibiae: 23–83 (53 ± 17) μ, 0.3–2.3 × diameter of metatibiae, tips incrassate to sharp; length variable, either approximately equal to gradually increasing distally, or abruptly doubling in length on central tibiae with setal length dimorphism present; longest ventral setae on metatibiae: 23– 43 (34 ± 7) μ, tips sharp. Length of metabasitarsus: 104–128 (115 ± 7) μ; metadistitarsus: 163–195 (177 ± 11) μ. Ratio of metadistitarsus to metabasitarsus less than 1.9:1, mean 1.54:1. *Pigmentation:* Color in life: Yellow throughout to body brown with yellow frons, legs and longitudinal stripe on

dorsomedial thoracic and abdomen. Dark specimens with tibiae usually yellow, to infrequently pro- and metatibiae as dark as dorsum, mesotibiae yellow; yellow specimens with tibiae concolorous with body to pro- and metatibiae brown, mesotibiae yellow. Slide-mounted specimens: Background of body dorsum variable, unicolorously pale to dark brown with paler frons and longitudinal area on dorso- medial terga of thorax and anterad of abdomen; dark pigmentation homogeneous to mottled (to 80 percent pigment density), when latter the pigmentation is density centers around each of the mesal pair of muscle attachment plates on the abdominal dorsum. Terga at bases of setae on frons and dorsal (major + minor) setae on abdomen concolorous with surrounding terga, to very subtly darker. Thoracic muscle attachment plates and dorsal muscle attachment plates of abdomen pale, vaguely conspicuous, to dark brown, reticulate with well defined borders, conspicuous. Spiracular plates and ventral ab- dominal sclerites light to dark brown, conspicuous. Siphunculi concolorous with surrounding terga. Cauda, anal and subgenital plates concolorous with abdominal terga, to slightly darker. Antennal segments V dusky; IV usually dusky on distal one-half or central one-third, frequently entirely dusky; III usually pale, infrequently subtly dusky on distal extreme when IV is entirely dusky; II very pale; I concolorous with frons. Tibiae variable, usually concolorously pale, despite dorsal pigmentation, often to moderate brown with pro- and metatibiae darker than mesotibiae; when metatibiae dark, rarely proximal one-third and ventrodistal tip subtly paler, or rarely pigmentation increasing evenly distally. Distitarsi dusky on distal one-half to three-quarters, when tibiae pale, to entirely brown with tibiae.

Ultimate Stadium Nymphs of Viviparous Apterae.—Slide-mounted specimens: Nonmorphometrics as described for viviparous apterae except lacking body dorsum pigmentation suite; abdominal terga membranous with dorsal (major + minor) setae, between muscle attachment plates, arising from distant scleroites. Mesonotum with 2 sclerotized plates extending from muscle attachment sites to engulf neighboring setal bases; plates usually heavily, to faintly, pigmented, diameter approximately equaling eye length.

Viviparous Alatae, Oviparae, Males, Fundatrices.—Unknown.

Diagnosis.—*Essigella* (*L.*) *eastopi* consists of pale to dark brown individuals. Dark specimens usually can be distinguished from other *Essigella* by having a dark brown body dorsum with a paler, longitudinal area on the dorsomedial region of the thoracic and anterad abdominal dorsum. The tibial pigmentation of *E.* (*L.*) *eastopi* is similar to that of *E.* (*L.*) *fusca* and *E.* (*L.*) *hillerislambersi,* and varies from all tibiae concolorously pale to a pigmentation suite in which the pro- and metatibiae are subtly to substantially darker than the mesotibiae; the latter is less prevalent in those *E.* (*L.*) *eastopi* with a dark body dorsum. When pale, the three *Lambersella* species can be difficult to separate. Some *E.* (*L.*) *eastopi* with short dorsal setae on the metatibiae (less than 1.2× tibial diameter) and *E.* (*L.*) *fusca* with long setae (greater than 3.0× tibial diameter) are exclusive. *Essigella* (*L.*) *hillerislambersi* is larger and can be separated from *E.* (*L.*) *eastopi* if antennal segment III exceeds 0.190 mm. Most morphometric characters overlap in these three species; reliable separation requires application of the discriminant functions in the key to the viviparous apterae [couplets 20 and 21, in that order].

Pale *E.* (*L.*) *eastopi* also can be confused with most other pale *Essigella*. They differ from *E.* (*E.*) *californica, E.* (*E.*) *hoerneri* and *E.* (*E.*) *pini* by having eight or more (see Figs. 1C–D), rather than six (Fig. 1F), dorsal (major + minor) setae on abdominal terga III–IV. *Essigella* (*L.*) *eastopi* lacks: the abdominal tergum I fusion of *E.* (*E.*) *essigi*; the protuberant, unusually distad primary rhinarium of *E.* (*E.*) *wilsoni*; and the exceptionally long metadistitarsus and short metabasi- tarsus of *E.* (*A.*) *kathleenae. Essigella* (*L.*) *eastopi* differs from *E.* (*E.*) *alyeska* by having three to five, rather than two, marginal setae on abdominal terga III–IV, and having large invasive, rather than small noninvasive, muscle attachment plates on the mesonotum of later stadia nymphs of apterae. Pale *E.* (*L.*) *eastopi* differ from pale *E.* (*E.*) *knowltoni* by being narrower, with sometimes sharply
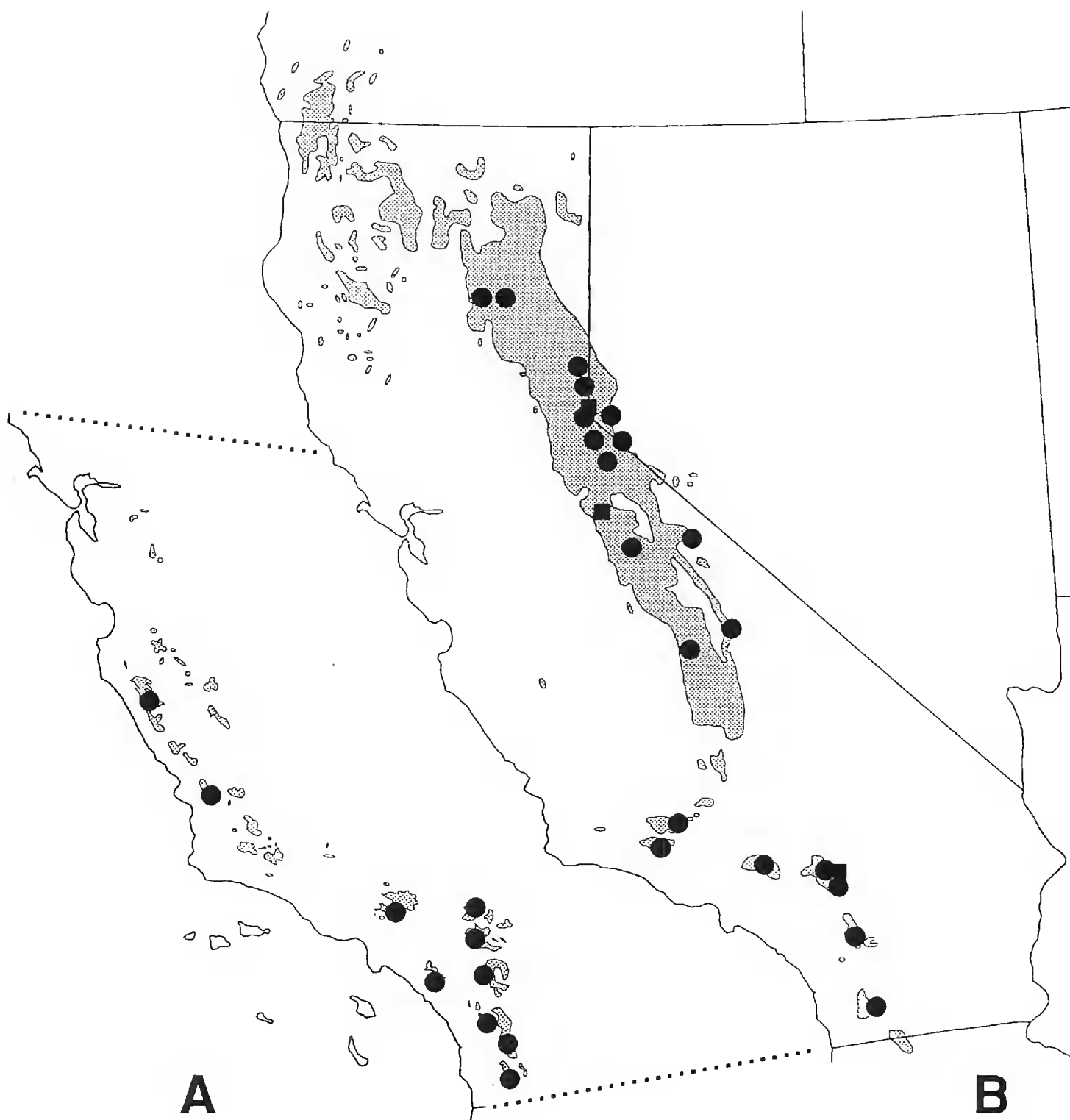
Figure 4.   Distribution of: A. *E.* (*L.*) *eastopi* [dots (JTS samples)], superimposed over the range of its host, *Pinus coulteri* [shaded]. B. *E.* (*L.*) *hillerislambersi* [dots (JTS samples), squares (nonJTS samples)], superimposed over the range of its host, *Pinus jeffreyi* [shaded].

tipped dorsal metatibial setae that frequently have an abrupt increase in length on the central part of the metatibiae. Pale *E.* (*L.*) *eastopi* with short dorsal metatibial setae (less than 0.7 × tibial diameter) can be especially similar to *E.* (*A.*) *kirki,* but have a metadistitarsus to metabasitarsus ratio of less than 1.70:1.

Range. — Coastal ranges of California, south of San Francisco Bay, to Mexico. The geographic range of *E.* (*L.*) *eastopi* is the most restricted of the genus (Fig. 4A).

Host. — *Pinus coulteri* D. Don. *Essigella* (*L.*) *eastopi,* on a subsection Sabinianae pine, is the only *E.* (*Lambersella*) that does not feed primarily on subsection Ponderosae pines, although *P. coulteri* does hybridize with *P. jeffreyi* of subsection Ponderosae.

Discussion. — *Essigella* (*L.*) *eastopi* is a relatively common species that is fairly

variable in morphology, especially in the length of the dorsal setae on the metatibiae. There are two semi-discrete, but intergrading, pigmentation morphs for its viviparous apterae. The general darkening of the background of the body dorsum on the darker morph can be considered a homoplasy with that of *E.* (*Essigella*); however, that morph's longitudinal, lightened dorsomedial area on the thorax and abdomen is an autapomorphy for *E.* (*L.*) *eastopi.*

Essigella (*L.*) *eastopi* is evolutionarily close to *E.* (*L.*) *fusca,* with which it shares several bivariate morphometric regressions. However, it appears to be morphologically closest to allopatric, rather than sympatric, populations of that species (see below). Dark individuals of *E.* (*L.*) *eastopi* generally have shorter setae than do paler specimens, which can approach *E.* (*L.*) *fusca* in appearance. Bivariant plotting of the longest dorsal seta on the central part of the metatibiae, versus metatibial length (unpublished data), suggests that *E.* (*L.*) *eastopi* may be a diminutive of *E.* (*L.*) *fusca voegtlini,* with respect to that derived regression line; it differs in this respect, however, from allopatric *E.* (*L.*) *fusca fusca,* which has relatively longer metatibiae. The isozymes and nucleic acids of populations of species in *E.* (*Lambersella*) should be examined, especially in the Tehachapi, San Gabriel and San Bernardino mountains of southern California; there, one large collection (D. J. Voegtlin 17; Running Springs, San Bernardino Co., on *P. coulteri*) is troublesome and may obscure clear separation of *E.* (*L.*) *eastopi* from *E.* (*L.*) *fusca voegtlini.*

Sorensen (1983) analyzed the relationships among taxa within *E.* (*Lambersella*) using principal component and discriminant function analyses on 35 morphometric traits. The principal component analysis (Sorensen 1983: section 2 PCA-1) showed that *E.* (*L.*) *eastopi* differed from *E.* (*L.*) *fusca,* as a species, in general-size, as represented as the first vector (which had uniformly high trait loadings and correlations). It was partially displaced from *E.* (*L.*) *fusca* on that vector, which gave the greatest separation to *E.* (*L.*) *hillerislambersi. Essigella* (*L.*) *eastopi* differed from sympatric *E.* (*L.*) *fusca voegtlini* on the second principal component vector, which chiefly involved the length of dorsal setae on the metatibiae; however, allopatric *E.* (*L.*) *fusca fusca* was intermediate between those two taxa on that vector. *Essigella* (*L.*) *eastopi* chiefly occupied the same size-independent principal component attribute space, defined by vectors 2 and 3 after size removal, as did sympatric *E.* (*L.*) *hillerislambersi.*

The discriminant function analysis (Sorensen 1983: section 2 DFA) echoed the findings of the principal component analysis, but with better group resolution and refined intergroup anagenic distances, as expected. Function 1 showed *E.* (*L.*) *eastopi* had greatest separation from *E.* (*L.*) *hillerislambersi,* with sympatric *E.* (*L.*) *fusca voegtlini* intermediate between those two, and allopatric *E.* (*L.*) *fusca fusca* yet intermediate between *E.* (*L.*) *eastopi* and *E.* (*L.*) *fusca voegtlini.* Discriminant function 2 showed *E.* (*L.*) *fusca voegtlini* separated from *E.* (*L.*) *eastopi,* *E.* (*L.*) *fusca fusca* and *E.* (*L.*) *hillerislambersi,* the three of which overlapped.

These analyses indicate a form of character displacement occurs among the three *E.* (*Lambersella*) species in California under sympatry (unpublished data).

Coded References to This Taxon.—Essigella (*L.*) *eastopi* has been referred to previously by: the coding "Sp. L" (Sorensen 1983 [but not section 2], 1987a, 1992b), "group B" (Sorensen 1983: section 2) and "EAST" (Sorensen 1983); and by the manuscript name *E.* "*eastopi*" in Sorensen (1983).

Etymology and Common Name.—The species is named for the aphidologist V. F. Eastop, who introduced me to the use and interpretation of bivariate plotting in aphid taxonomy. Common name: Eastop's Coulter pine needle aphid.

Material Examined.—CALIFORNIA. *LOS ANGELES Co.:* hwy 2, 7 km NE of jct with Mt Wilson Rd, San Gabriel Mts, 1530 m, 18 Sep 1977, JTS 77I51, *P. coulteri,* (apt.). *MONTEREY Co.:* Cone Peak Rd, 2 km N of jct with Nacimento-Fergusson Rd, Los Padres Natl Forest, 910 m, 4 Sep 1977, JTS 77I9, *P. coulteri,* (apt.). *ORANGE Co.:* above Santiago Peak Rd, 10 km N of jct with hwy 74, Cleveland Natl Forest, 1220 m, 10 Sep 1977, JTS 77122, *P. coulteri,* (apt.). *RIVERSIDE Co.:* Keen Camp Summit on hwy 74, 3 km N of Mountain Center, San Bernardino Natl Forest, 1500 m, 9 Sep 1977, JTS 77I20, *P. coulteri,* (apt.). *SAN BERNARDINO Co.:* "view" Picnic Area on hwy 18, W of Rimforest, San Bernardino Natl Forest, 1620 m, 17 Sep 1977, JTS 77I44, *P. coulteri,* (apt.); 7 km W of Barton Flat on hwy 38, 1950 m, 16 Sep 1977, JTS 77I36, *P. coulteri,* (apt.). *SAN DIEGO Co.:* 5 km S of Julian, Harrison Springs Rd, 1460 m, 12 Sep 1977, JTS 77129, *P. coulteri,* (apt.); (type series) 8 km N of Mt Laguna on hwy S1, 1700 m, 12 Sep 1977, JTS 77I32, *P. coulteri,* (apt.); Mt Palomar Rd (S6), 3 km S of Mt Palomar, 1530 m, 11 Sep 1977, JTS 77I27, *P. coulteri,* (apt.). *SAN LUIS OBISPO Co.:* Cuesto Ridge Botanical Area, nr La Cuesta Summit on hwy 101, N of San Luis Obispo, 730 m, 5 Sep 1977, JTS 77I14, *P. coulteri,* (apt.).

Essigella (Lambersella) fusca fusca Gillette & Palmer 1924, NEW STATUS

Essigella fusca Gillette & Palmer, 1924: 6, Ann. Entomol. Soc. Am., 17: 6–9.
Essigella agilis Hottes, 1957: 71, Proc. Biol. Soc. Wash., 70: 71–73. NEW SYNONYM.
Essigella palmerae Hottes, 1957: 96, Proc. Biol. Soc. Wash., 70: 96–98. NEW SYNONYM.

Primary Types.—Lectotype, vivip. apt., on slide alone; slide data: *"Essigella fusca,* apt. viv., Holotype, C. P. Gillette & M. A. Palmer, Mt'd. in Damar in xylene/U.S. Nat. Mus., No. 41953/On *Pinus ponderosa* var. *scopulorum,* Rocky Mt. Nat. Park (Grags Hill [sic], near Bald Pate Inn) Colo., 7-18-23, Coll. M. A. Palmer, Colo. Agr. Exp. Ac. No. 3422/[on back] lectotype, J. T. Sorensen, 1982." Lectotype deposited in the U.S. National Museum of Natural History, Washington, D.C.

There is a problem regarding type designation; Hottes (1957: 88) confusingly mentions both a lectotype and holotype for this species. A slide marked "holotype" exists. In the original description, Gillette & Palmer (1924: 6–9) do not designate a primary type, but later (Gillette & Palmer 1931: 840) state "Types in the U.S. Nat. Mus., Cat. No. 41953; Paratypes in collection of Colo. Agr. Exp. Sta." Palmer (1952: 15) under the heading "Type" also lists that number. In addition, 2 slides (allo- and morphotypes) bear the number, precluding identification of any individual as lectotype, based on the number alone. Because I cannot tell from Hottes' publication (1957) that he clearly was designating a lectotype, I presently designate the "holotype" specimen as lectotype, following Hottes' mention of it. I have added the lectotype label listed above to the back of that slide. Unfortunately, the specimen lacks metalegs and is obscured by debris, but it is recognizable as *E. (L.) fusca.*

Viviparous Apterae.—*Morphology:* Body length: 1.79–2.39 (2.09 ± 0.18) mm. HEAD: Primary rhinarium on terminal antennal segment (V) not exceptionally distad, distance from tip of processus terminalis to distal face of rhinarial rim greater than 0.5× diameter of rhinarium; distal face of rhinarial rim usually oblique to longitudinal axis of antennal segment; rhinarial membrane not conspicuously

protuberant. Length of antennal segment V: 118–145 (130 ± 7) μ, processus terminalis: 30–48 (37 ± 4) μ; IV: 73–100 (88 ± 8) μ; III: 135–180 (159 ± 12) μ; II: 65–95 (76 ± 7) μ. Length of longest setae on frons: 35–80 (58 ± 11) μ, tips incrassate to sharp. Head width: 245–316 (293 ± 17) μ. Length of stylets: 602–867 (756 ± 62) μ; ultimate rostral segment: 78–98 (90 ± 5) μ, rostral tip reaching abdominal terga I–II, infrequently III, in dorsal view through slide-mounted specimens. Head + pronotum fused, total length: 383–479 (424 ± 25) μ. THORAX: Meso + metanota fused, total length: 326–459 (400 ± 31) μ. ABDOMEN: Tergum I free, length: 138–184 (162 ± 14) μ; terga II–VII fused, VIII free. Maximum distal width of flange on siphunculi: 38–50 (45 ± 3) μ; siphunculi truncated conical, protrusion 0.2–0.6 × maximum distal width. Ventral abdominal sclerites on segments III–IV subquadrate, subelliptical to sublinear, often centrally constricted; length: 48–90 (73 ± 10) μ, 1.2–2.6 × diameter of metatibiae. Dorsal (major + minor) setae (see Figs. 1C–D) on abdominal terga III–IV: 8–12 (11 ± 1), tips sharp, in 2 (rarely 1) rows with setae in regular position, lateral-most minor dorsal seta in anterad row; marginal setae 3–5, usually 4 per segment each side. Setae on abdominal tergum VIII: 8–11 (10 ± 1), length: 40–80 (64 ± 9) μ, tips incrassate to sharp, in 1–2 rows. Cauda broadly rounded; caudal protuberance absent to poorly developed; length of longest caudal setae: 83–128 (102 ± 13) μ, tips sharp. LEGS: Length of metafemora: 581–898 (762 ± 95) μ; metatibiae: 755–1132 (971 ± 104) μ; longest dorsal setae on central one-third of metatibiae: 50 (rarely 15)–120 (76 ± 18) μ, 0.5–3.6, usually 1.2–2.8, × diameter of metatibiae, tips usually incrassate to blunt, occasionally sharp; length variable, either approximately equal along tibiae, gradually increasing distally, or abruptly doubling in length on central tibiae with setal length dimorphism present; longest ventral setae on metatibiae: 29–68 (41 ± 9) μ, tips sharp. Length of metabasitarsus: 130–170 (148 ± 12) μ; metadistitarsus: 170–233 (205 ± 16) μ. Ratio of metadistitarsus to metabasitarsus less than 1.9:1, mean 1.39:1. *Pigmentation:* Color in life: Head and thorax yellow-brown, abdomen green, pro- and metatibiae light to dark brown with mesotibiae yellow-brown, dorsal spots brown; or frequently green-yellow to straw yellow, rarely gray throughout. Slide-mounted specimens: Background of body dorsum pale to moderate brown, often mottled, rarely dark brown (usually to 30, rarely to 80, percent pigment density). Terga at bases of setae on frons and dorsal (major + minor) setae on abdomen subtly to substantially darker than surrounding terga. Thoracic muscle attachment plates and dorsal muscle attachment plates of abdomen varying from moderate to dark brown, conspicuous, often reticulate, sometimes with surrounding tergum more heavily mottled than elsewhere, to pale, inconspicuous. Spiracular plates and ventral abdominal sclerites usually moderate to dark brown, conspicuous, to pale, inconspicuous. Siphunculi concolorous with surrounding terga. Cauda, anal and subgenital plates concolorous with abdominal terga, to slightly darker. Antennal segments V and IV moderate to dark brown, usually concolorous, but frequently paler proximally, infrequently also paler distally; III usually moderate to dark brown on distal one-third, rarely one-half, remainder pale, often entirely pale; II usually subtly darker than proximal III, seldom conspicuously darker, rarely concolorous with proximal III; I usually concolorous with frons, to conspicuously darker. Tibiae variable, usually pro- and metatibiae evenly light to dark brown with mesotibiae substantially paler, sometimes dark pro- and metatibiae paler on proximal and distal tips to one-fourth; commonly all tibiae concolorously pale when body dorsum pale. Distitarsi usually evenly light to dark brown with pro- and metatibiae, to dusky with paler proximal tip when tibiae pale.

Ultimate Stadium Nymphs of Viviparous Apterae. — Slide-mounted specimens: Nonmorphometrics as described for viviparous apterae except lacking body dorsum pigmentation suite; abdominal terga membranous with dorsal (major + minor) setae, between muscle attachment plates, arising from distinct scleroites. Mesonotum with 2 sclerotized plates extending from muscle attachment sites to engulf neighboring setal bases; plates usually distinct, moderately to darkly pigmented, diameter approximately equaling eye length.

Viviparous Alatae. — Slide-mounted specimens: Nonmorphometrics as described for viviparous apterae except lacking body dorsum pigmentation suite; abdominal terga normally membranous, dorsal (major + minor) setae between muscle attachment plates frequently arising from distinct scleroites; antennal segments often as dark as tibiae, except proximal one-fifth of III pale. Antennal segment III with 0–5, IV with 0–1, secondary rhinaria. Epicranial suture absent. Forewing medius with single furcation arising on proximad one-third of vein; cubital base usually arising distad, infrequently proximad, on subcosta with distance between anal and cubital bases on subcosta usually relatively large, ca. 30–40 percent or more of anal vein length; usually medius, sometimes cubitus and anal veins faint, vague to absent. Abdominal terga frequently with irregular sclerites that engulf or join muscle attachment plates and dorsal (major + minor) setal bases or scleroites.

Oviparae.—Slide-mounted specimens: Nonmorphometrics as described for viviparous apterae except abdominal terga II–VI fused, lightly to moderately sclerotic, including pleural areas, but VII and VIII free; dorsal demarcations of anterad terga rarely evident; siphunculi usually incorporated into sclerotic dorsum, to free; dorsal abdominal muscle attachment plates unicolorous. Pseudorhinaria on metatibiae irregular, 9–27.

Males.—Slide-mounted specimens: Nonmorphometrics as described for viviparous apterae except body slightly smaller, with slightly longer antennae and tibiae; dorsal demarcations of abdominal terga evident. Antennal segment III with 13–15, IV with 8–10, secondary rhinaria.

Fundatrices.—Slide-mounted specimens: Nonmorphometrics as described for viviparous apterae except siphunculi absent; longest dorsal setae on central part of metatibiae 0.8–1.0× tibial diameter.

Diagnosis.—Pigmented *Essigella* (*L.*) *fusca* can be distinguished from all *Essigella,* except *E.* (*L.*) *hillerislambersi* and *E.* (*L.*) *eastopi,* by the tibial pigmentation suite in which the pro- and metatibiae are often substantially darker than the mesotibiae. *Essigella* (*L.*) *fusca* lack the completely developed pigmentation for the body dorsum shown by some *E.* (*L.*) *eastopi,* but cannot be separated reliably from *E.* (*L.*) *hillerislambersi* by pigmentation. Pale *E.* (*L.*) *fusca, E.* (*L.*) *eastopi* and *E.* (*L.*) *hillerislambersi* can be separated from other pale *Essigella* by the diagnostics given for pale *E.* (*L.*) *eastopi.* Pale *E.* (*L.*) *fusca* have longer dorsal setae on the metatibiae (greater than 1.2× tibial diameter) than some *E.* (*L.*) *eastopi,* and a shorter antennal segment III than *E.* (*L.*) *hillerislambersi;* but these differences are indiscrete. Reliable separation of these *Lambersella* species requires application of the discriminant functions in the key to the viviparous apterae [couplets 20 and 21, in that order].

As subspecies, *E.* (*L.*) *fusca fusca* and *E.* (*L.*) *fusca voegtlini* are morphologically indiscrete, with clinal univariate characters; their separation is locality dependent, but they can be classified using the discriminant function in the key to the viviparous apterae [couplet 22]. In *Essigella* (*L.*) *fusca fusca,* the metatibiae and antennal segment V are generally longer, and the dorsal setae on the metatibiae are generally shorter, than in *E.* (*L.*) *fusca voegtlini.*

Synonyms.—*Essigella agilis* Hottes, NEW SYNONYM: holotype, vivip. apt., on slide with 4 other specimens, holotype shown by arrow (7–8 o'clock position); data: COLORADO. *MESA Co.:* Glade Park, 26 Jun 1956, F. C. Hottes, *Pinus ponderosa* Lawson. *Essigella agilis* holotype deposited in NMNH.

Essigella palmerae Hottes, NEW SYNONYM: holotype, vivip. alat., on slide with morphotype vivip. apt.; data: ARIZONA. *PIMA Co.:* Summerhaven, 13 Jun 1954, F. C. Hottes, *Pinus ponderosa. Essigella palmerae* holotype deposited in NMNH.

Range.—Southern British Columbia, south: (in the east) through the Rocky Mountains to Arizona, New Mexico and into Mexico; (in the west) to northern and eastern Oregon, but not California or southwestern Oregon (Fig. 5). [For species, see *E.* (*L.*) *f. voegtlini* also.]

Hosts.—Subsection Ponderosae pines, principally *Pinus ponderosa* Lawson, but also *P. ponderosa* var. *arizonica* Engelmann, *P. engelmannii* Carriére, and *P. leiophylla* Schiede & Deppe (latter, subsection Leiophyllae). Assuming the identification is correct, a reputed collection from *Callitris drummondii* Betham & Hooker f. ex F. Mueller (Cupressaceae), listed in Blackman & Eastop (in press) as "BMNH colln, leg. H. G. Walker" [R. L. Blackman, personal communication], and in Walker et al. (1978: 588) under that host as "31/I/71 Moderate (VFE)," is undoubtedly from a nonresident host in one of Walker's many Los Angeles

Arboretum samples; most identifications of *Essigella* to species that are listed in Walker et al. (1978) are questionable, because only Hottes' (1957) key was available at the time. [For species, see *E. (L.) f. voegtlini* also.]

Discussion.—*Essigella (L.) fusca* is a common and morphologically variable species. Sorensen (1983) analyzed the *E. (Lambersella)* species; see the discussion of *E. (L.) eastopi* for a brief summary. That study also analyzed *E. (L.) fusca* itself, after breaking it further into geographic subunits for other principal component analyses (Sorensen 1983: section 2 PCA-2, PCA-3). Within *E. (L.) fusca*, general-size variance (Sorensen 1983: section 2 PCA-2, vector 1) dominated any difference among populations. There was, however, a general east-west gradient (Sorensen 1983: section 2 PCA-2, vector 2) with longer dorsal setae on the metatibiae, and shorter metatibiae occurring in the west [*E. (L.) f. voegtlini*], and the opposite combination in the more eastern portions of the range [*E. (L.) f. fusca*]. The next most dominant vector (Sorensen 1983: section 2 PCA-2, vector 3) in that analysis suggested a very rough north-south morphocline among non-Californian populations [*E. (L.) f. fusca*], which the Californian material [*E. (L.) f. voegtlini*] spanned.

When material from California was omitted from those analyses to improve resolution further, general-size variance (Sorensen 1983: section 2 PCA-3, vector 1) still dominated interpopulational differences among the nonCalifornian populations. However, subordinate to that, nonCalifornian populations [*E. (L.) f. fusca*] showed a general north-south gradient (Sorensen 1983: section 2 PCA-3, vector 2) that involved the length of dorsal setae on the metatibiae and lateral setae on the body, plus the number of dorsal (major + minor) setae on the abdomen; this vector, in the absence of interference from *E. (L.) f. voegtlini*, oriented to, and improved the resolution of, the variance revealed in the second vector of the previous analysis (Sorensen 1983: section 2 PCA-2, vector 3). The third vector (Sorensen 1983: section 2 PCA-3, vector 3) for the nonCalifornian populations showed mostly intrapopulational variance.

With respect to qualitative traits, *E. (L.) fusca fusca* populations from Arizona and New Mexico frequently are slightly paler, with slightly darker metatibiae that sometimes show both their distal and proximal ends to be paler. This southwestern material, however, is not considered sufficiently distinct to warrant recognition with subspecific status on the basis of either quantitative or qualitative traits.

Coded References to This Taxon.—*Essigella (L.) fusca fusca* has been referred to previously by: the coding "Sp. M" (Sorensen 1983 [but not section 2], 1987a, 1992b), "group D" (Sorensen 1983: section 2) and "FUSC" (Sorensen 1983); and by the name *E. fusca fusca* in Sorensen (1983).

Etymology and Common Name.—"*Fusca,*" from the Latin "*fuscus,*" meaning "dusky," "dark" or "swarthy" (Brown 1978); apparently with reference to ". . . having dorsum of abdomen dark in color in apterous virgogenia" (Gillette & Palmer 1924: 8). Common name: the dusky ponderosa pine needle aphid; although Palmer (1952:14) refers to this species as "The Brown and Green Pine needle Aphid," the common name indicated here is more appropriate and less confusing because other *Essigella* are brown and green.

Material Examined.—[*E. (L.) fusca fusca* only :] ARIZONA. *APACHE Co.:* 10 km N of Lupton on hwy 12 (= 166), 2070 m, 11 Sep 1978, JTS 78I18, *P. ponderosa*, (apt.). *COCHISE Co.:* nr Rustler
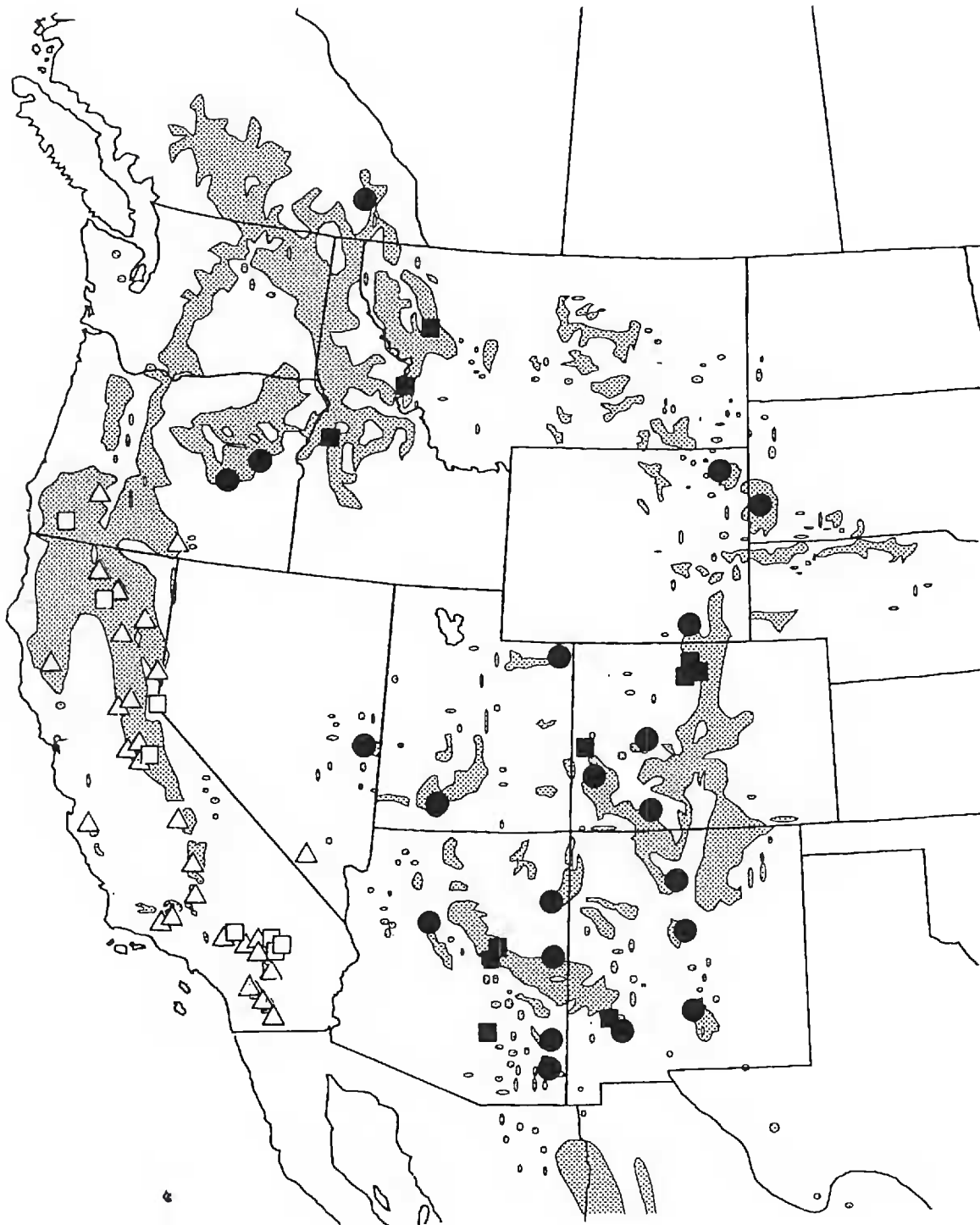
Figure 5.   Distribution of *E.* (*L.*) *fusca fusca* [black dots (JTS samples), black squares (nonJTS samples)] and *E.* (*L.*) *fusca voegtlini* [white triangles (JTS samples), white squares (nonJTS samples)], superimposed over the range of its principal host, *Pinus ponderosa* [shaded].

Park, Chiricahua Mts, 2500 m, 16 Sep 1978, JTS 78I47, *P. ponderosa,* (apt.). *COCONINO Co.:* 9 km W of Williams on hwy 66, 2070 m, 9 Sep 1978, JTS 78I5, *P. ponderosa,* (apt.). *GILA Co.:* Pine, 17 May 1978, C. F. & C. S. Smith, CFS 78-31, *Pinus* sp., (apt.). *GRAHAM Co.:* SW of Stafford on hwy 366, 1830 m, 15 Sep 1978, JTS 78I36, *P. leiophylla,* (apt.); same but 1980 m, JTS 78I37, *P. ponderosa* var. *arizonica,* (apt.). *NAVAJO Co.:* Mogollon Rim Rd, 8 km SW of Showlow, 2070 m, 10 Sep 1978, JTS 78I13, *P. ponderosa,* (apt.). *PIMA Co.:* Summerhaven, 13 Jun 1954, F. C. Hottes, (alat.). *COUNTY UNCERTAIN:* Sitgreaves Natl Forest, 18 Jun 1969, D. T. Jennings, *P. ponderosa,* (alat.). COLORADO. *ARCHULETA Co.:* 25 km W of Pagosa Springs on hwy 160, 2140 m, 8 Aug 1978, JTS 78H50, *P. ponderosa,* (apt.). *GUNNISON Co.:* 16 km NW of Kebler Pass, 2440 m, 13 Aug 1978, JTS 78H75, *P. ponderosa,* (apt.). *LARIMER Co.:* (lectotype) Bald Pate Inn, nr Craig's Hill, Rocky Mt Natl Park, 12 Jul 1923, M. A. Palmer, CAES 3420, *P. ponderosa,* (apt.); (paratype) Craigs, Estes Park, 27 Jul 1923, M. A. Palmer, CAES 3430, *P. ponderosa,* (alat.); (type) Craigs, nr twin Sisters Mt, 27 Jul 1923, M. A. Palmer, CAES 3430/USNM 41953, *P. ponderosa,* (alat.); Estes Park, 1 Sep 1922, F. C. Hottes, CAES 3312/USNM 41953, *P. ponderosa,* (ovip., male); same but 24 Jul 1921, C. P. Gillette, CAES 2804, (apt.). *MESA Co.:* Glade Park, 26 Jun 1956, F. C. Hottes, *P. ponderosa,* (apt.); Carson Hole, 3/8 Aug 1956, (apt.). *SAN MIGUEL Co.:* 6 km NE of Placerville on hwy 62, 2320 m, 7 Aug 1978,

JTS 78H43, *P. ponderosa*, (apt.). IDAHO. *IDAHO Co.:* Deep Creek, nr Old Warrior's Face, Bitteroot Natl Forest, 16 Aug 1979, D. J. Voegtlin, DJV 691, *P. ponderosa*, (apt.). *VALLEY Co.:* McCall, 23 Sep 1956, M. J. Forsell, *P. ponderosa*, (apt., alat., ovip., male). MONTANA. *MISSOULA Co.:* Big Larch Cmpgd, Seeley Lake, Lola Natl Forest, NE of Missoula, 20 Aug 1979, D. J. Voegtlin, DJV 713, *P. ponderosa*, (apt.). NEVADA. *WHITE PINE Co.:* Wheeler Peak, 2750 m, 26 Aug 1978, JTS 78H153, *P. ponderosa*, (apt.). NEW MEXICO. *BERNALILLO Co.:* 2 km NW of San Antinito on hwy 44, 2290 m, 12 Sep 1978, JTS 78I20, *P. ponderosa*, (apt.). *OTERO Co.:* Cloudcroft, hwy 82, 2710 m, 13 Sep 1978, JTS 78I25, *P. ponderosa*, (apt.). *SANTA FE Co.:* 20 km NE of Santa Fe on hwy 475, 2680 m, 10 Aug 1978, JTS 78H59, *P. ponderosa, (apt.)*. *SIERRA Co.:* 3 km W of Kingston on hwy 90, 2140 m, 14 Sep 1978, JTS 78I32, *P. ponderosa*, (apt., alat.). *COUNTY UNCERTAIN:* Gila Natl Forest, 19 Jul 1965, H. G. Kinzer, *P. ponderosa*, (alat.); same but 1 Nov 1967, (apt.). OREGON. *BAKER Co.:* 11 km W of Unity on hwy 26, 20 Jul 1978, JTS 78G112, *P. ponderosa*, (alat.). *HARNEY Co.:* 20 km N of Burns on hwy 395, 20 Jul 1978, JTS 78G117, *P. ponderosa*, (apt.). SOUTH DAKOTA. *LAW-RENCE Co.:* 20 km S of Deadwood on hwy 385, 1650 m, 18 Aug 1978, JTS 78H98, *P. ponderosa*, (apt.). UTAH. *DAGGETT Co.:* 21 km S of Manila on hwy 44, 2350 m, 24 Aug 1978, JTS 78H135, *P. ponderosa*, (apt.). *KANE Co.:* 50 km SE of Cedar City on hwy 14, 2560 m, 5 Aug 1978, JTS 78H28, *P. ponderosa*, (apt.). WYOMING. *ALBANY Co.:* hwy 287, 2 km N of state border, 15 Aug 1978, JTS 78H93, *P. ponderosa*, (apt.). *CROOK Co.:* 6 km W of Devil's Tower Jct on hwy 14, 1100 m, 19 Aug 1978, JTS 78H104, *P. ponderosa*, (apt.). CANADA. *BRITISH COLUMBIA:* Fairmont Hotsprings, hwy 93, 17 Jul 1978, JTS 78G91, *P. ponderosa*, (apt.). MEXICO. *PUEBLA:* Puebla, km 43 Corr. Fed., 11 Jun 1983, A. L. Munuz, 267, *Pinus* sp., (apt.). *STATE UNCERTAIN:* Sierra Largo, at El Passo, 12 Jun 1966, Eads & Rood, *Pinus* sp., (apt.).

Essigella (Lambersella) fusca voegtlini, NEW SUBSPECIES

Essigella "fusca voegtlini" Sorensen, 1983: 89 (unpublished manuscript name) Ph.D. Thesis, University of California at Berkeley, Berkeley, California. 605 p.

Type Series.—Holotype, vivip. apt., on slide with 2 paratype vivip. apt., the holotype is only complete specimen on the slide, at top (1 o'clock position); data: CALIFORNIA. *FRESNO Co.:* jct hwys 180 & 245, 1620 m, 13 Aug 1977, J. T. Sorensen (77H9), *Pinus ponderosa.* Holotype deposited in The Natural History Museum, London. Paratypes (all same data as holotype): 18 vivip. apt., on 5 slides including holotype slide. Paratype slides deposited: 1 slide in NMNH, Washington, D.C.; 1 slide in CNC, Ottawa, Ontario; 2 slides in Sorensen collection.

Viviparous Apterae.—Morphology: As *E. (L.) fusca fusca*, except as follows: Body length: 1.88–2.21 (2.04 ± 0.09) mm. HEAD: Length of antennal segment V: 105–135 (121 ± 8) μ, processus terminalis: 30–40 (36 ± 3) μ; IV: 70–100 (85 ± 7) μ; III: 128–178 (147 ± 14) μ; II: 65–85 (73 ± 5) μ. Length of longest setae on frons: 44–88 (59 ± 12) μ. Head width: 275–311 (289 ± 10) μ. Length of stylets: 551–857 (732 ± 66) μ; ultimate rostral segment: 84–95 (89 ± 3) μ. Total length of fused head + pronotum: 377–449 (419 ± 16) μ. THORAX: Total length of fused meso + metanota: 347–428 (389 ± 19) μ. ABDOMEN: Tergum I length: 138–179 (157 ± 10) μ. Maximum distal width of flange on siphunculi: 30–48 (39 ± 5) μ. Ventral abdominal sclerite length: 44–80 (69 ± 9) μ. Dorsal (major + minor) setae (see Figs. 1C–D) on abdominal terga III–IV: 8–12 (10 ± 1); marginal setae 4–5 per segment each side. Setae on abdominal tergum VIII: 8–10 (8 ± 1), length: 45–100 (69 ± 14) μ. Length of longest caudal setae: 80–120 (98 ± 9) μ. LEGS: Length of metafemora: 612–831 (732 ± 62) μ; metatibiae: 806–1061 (941 ± 75) μ; longest dorsal setae on central one-third of metatibiae: 58–135 (103 ± 19) μ; longest ventral setae on metatibiae: 38–83 (52 ± 11) μ. Length of metabasitarsus: 128–155 (141 ± 9) μ; metadistitarsus: 173–223 (198 ± 11) μ. Mean ratio of metadistitarsus to metabasitarsus: 1.40:1. *Pigmentation:* As *E. (L.) fusca fusca.*

Diagnosis.—See the *E. (L.) fusca fusca* diagnosis, and couplet 22 in the key to the viviparous apterae.

Range. —California, southwestern Oregon, extreme western Nevada (Fig. 5). [For species, see *E. (L.) f. fusca* also.]

Hosts. —Subsection Ponderosae pines, principally *Pinus ponderosa* Lawson, but also *P. jeffreyi* Greville & Balfour and *P. coulteri* D. Don (latter, subsection Sabinianae); single collections from *P. sabiniana* Douglass (77F15), *P. monophylla* Torrey & Frémont (77H3), *P. contorta murrayana* Greville & Balfour (R. Luck sample) and *P. quadrifolia* Parlatore (77I19) are probably not resident. [For species, see *E. (L.) f. fusca* also.]

Discussion. —*Essigella (L.) fusca voegtlini,* although a gradient subspecies [see discussion under *E. (L.) f. fusca*], is named to recognize the morphometric problems of *E. (L.) fusca* in sympatry with *E. (L.) eastopi,* and especially *E. (L.) hillerislambersi. Essigella (L.) f. voegtlini* [and *E. (L.) f. fusca* to a very much lesser extent] shows a common dimorphism of length for the dorsal setae on the metatibiae. The dimorphism is evident in either of two forms: (a) on a given individual, as an abrupt transition from shorter to longer setae along the central portion of the dorsum of the metatibia; or (b) among various individuals in, or among, populations as the length of the longest setae on the central portion of the dorsum of the metatibia.

This dimorphism causes a gap along a regression line of length of these setae when plotted against metatibial length (Sorensen 1983). Interestingly, the length of the dorsal setae of the metatibiae on *E. (L.) hillerislambersi* correspond to this gap, indicating a character displacement in sympatry. These setal lengths do not appear to be influenced by host on *E. (L.) f. voegtlini.*

Coded References to This Taxon. —*Essigella (L.) fusca voegtlini* has been referred to previously by: the coding "Sp. N" (Sorensen 1983 [but not section 2], 1987a, 1992b), "group C" (Sorensen 1983: section 2) and "VOEG" (Sorensen 1983); and by the manuscript name *E. "fusca voegtlini"* in Sorensen (1983).

Etymology and Common Name. —The California subspecies is named for aphidologist D. J. Voegtlin, and his ever-present beard. Common name: Voegtlin's dusky ponderosa pine needle aphid.

Material Examined. —[*E. (L.) fusca voegtlini* only :] CALIFORNIA. *BUTTE Co.:* Feather River Cyn, 5 km NE of jct of hwy 70 & Cherokee Rd, 26 Jun 1977, JTS 77F15, *P. sabiniana,* (apt.). *CALAVERAS Co.:* 18 km E of Arnold on hwy 4, 1680 m, 17 Jul 1977, JTS 77G46, *P. ponderosa,* (apt.); 2 km NE of Murphys on hwy 4, 670 m, 17 Jul 1977, JTS 77G47, *P. ponderosa,* (apt.). *EL DORADO Co.:* Georgetown, 29 May 1977, J. T. Sorensen, *P. ponderosa,* (apt.). *FRESNO Co.:* (type species) jct of hwys 180 & 245, 1620 m, 13 Aug 1977, JTS 77H9, *P. ponderosa,* (apt.). *INYO Co.:* jct of Lake Sabrina Rd & Southern Calif. Edison Plant 2 Rd, nr Bishop, 2130 m, 1 Aug 1977, JTS 77H3, *P. monophylla,* (apt.). *KERN Co.:* Tehachapi Mtn Park, S of Tehachapi, 1980 m, 19 Sep 1977, JTS 77I60, *P. ponderosa,* (apt., ovip.); same but JTS 77I61, *P. jeffreyi,* (apt.); Tiger Flat Rd, N of hwy 155, nr Alta Sierra, 1890 m, 20 Sep 1977, JTS 77I65, *P. ponderosa,* (apt.). *LAKE Co.:* 5 km S of Lake Pillsbury, Elk Mt Rd, 640 m, 24 Jul 1977, JTS 77G56, *P. jeffreyi,* (apt.). *LASSEN Co.:* 7 km SW of Susanville on hwy 36, 1460 m, 4 Jul 1977, JTS 77G13, *P. jeffreyi,* (apt.). *LOS ANGELES Co.:* Camp Baldy, 5 Dec 1956, J. MacSwain, "on fir," (apt.); hwy 2, 7 km NE of jct with Mt Wilson Rd, San Gabriel Mts, 1530 m, 18 Sep 1977, JTS 77I51, *P. coulteri,* (apt.). *MONTEREY Co.:* Plaskett Ridge Rd, Los Padres Natl Forest, 1040 m, 4 Sep 1977, JTS 77I11, *P. ponderosa,* (apt.). *PLUMAS Co.:* 2 km SE of Graeagle on hwy 89, 1310 m, 26 Jun 1977, JTS 77F10, *P. ponderosa,* (apt.); Halsted Cmpgd, Plumas Natl Forest, 19 km NE of Beldon on hwy 70, 790 m, 26 Jun 1977, JTS 77F13, *P. ponderosa,* (apt.). *RIVERSIDE Co.:* 2 km N of Paradise Valley on hwy 74, 1500 m, 9 Sep 1977, JTS 77I19, *P. quadrifolia,* (apt.). *SAN BERNARDINO Co.:* 7 km W of Barton Flat on hwy 38, 1950 m, 16 Sep 1977, JTS 77I36, *P. coulteri,* (apt.); San Bernardino Natl Forest, "view" Picnic Area on hwy 18, W of Rimforest, 1610 m, 17 Sep 1977, JTS 77I43, *P. ponderosa,* (apt.); same but 1620 m, JTS 77I44,

P. coulteri, (apt., alat.); same but Barton Flat, 29 Aug 1972, D. J. Voegtlin, DJV 67, (apt.); same but Camp Angeles, 29 Aug 1972, D. J. Voegtlin, DJV 66, *P. ponderosa,* (apt.); same but Dogwood, 28 Aug 1972, DJV 25, (apt.); same but Snow Valley, DJV 69, *P. jeffreyi,* (apt.); same but Running Springs, 4 Aug 1973, DJV 77, *P. coulteri,* (apt.); San Bernardino Mts, nr jct of Jenks Lake Rd & hwy 38, 2010 m, 16 Sep 1977, JTS 77I35, *P. ponderosa,* (apt.); same but 2 km S of jct of hwy 38 & Jenks Lake Rd, 2200 m, JTS 77I39, *P. jeffreyi,* (apt.). *SAN DIEGO Co.:* 2 km E of Mt Palomar on hwy S6, 1650 m, 11 Sep 1977, JTS 77I28, *P. attenuata,* (apt.); 5 km S of Julian, Harrison Springs Rd, 1460 m, 12 Sep 1977, JTS 77I29, *P. coulteri,* (apt.); lake Cuyamaca, nr Cuyamaca State Park, 1800 m, 12 Sep 1977, JTS 77I30, *P. ponderosa,* (apt.); Mt Palomar Rd (S6), 3 km S of Mt Palomar, 1530 m, 11 Sep 1977, JTS 77I27, *P. coulteri,* (apt.). *SHASTA Co.:* 2 km W of Fall River Mills on hwy 299, 21 Jul 1978, JTS 78G123, *P. ponderosa,* (apt.); Hat Creek, 24 Jun 1955, E. O. Essig, *P. ponderosa,* (apt.). *SISKIYOU Co.:* Edson Creek access Rd, Shasta Natl Forest, 8 km W of Bartel on hwy 89, 1160 m, 3 Jul 1977, JTS 77G10, *P. jeffreyi,* (apt.). *TUOLUMNE Co.:* 2 km E of Groveville on hwy 120, 910 m, 30 Jul 1977, JTS 77G63, *P. ponderosa,* (apt.); Yosemite Natl Park, 17 May 1938, E. O. Essig, *P. ponderosa,* (fund.). *VENTURA Co.:* Mt Pinos Summit, 2680 m, 18 Sep 1977, JTS 77I55, *P. jeffreyi,* (apt.); Reyes Peak Rd, 10 km E of Pine Summit on hwy 33, 2200 m, 19 Sep 1977, JTS 77I59, *P. jeffreyi,* (apt.). *COUNTY UNCERTAIN:* Lake Tahoe, 16 Jul 1969, R. Luck, *P. contorta murrayana,* (apt.); same but 17 Jul 1969, *P. jeffreyi,* (apt.). NEVADA. *CLARK Co.:* Charleston Mts, Lee Canyon Ski Area, 2590 m, 4 Aug 1978, JTS 78H18, *P. ponderosa,* (apt.). OREGON. *JACKSON Co.:* 21 km S of Union Creek on hwy 62, 5 Jul 1978, JTS 78G15, *P. ponderosa,* (apt., alat.). *JOSEPHINE Co.:* Grant's Pass, 2 Sep 1914, H.F.W., *P. ponderosa,* (apt.). *LAKE Co.:* 28 km N of Lakeview on hwy 395, 20 Jul 1978, JTS 78G119, *P. ponderosa,* (apt.).

Essigella (Lambersella) hillerislambersi, NEW SPECIES

Essigella "hillerislambersi" Sorensen, 1983: 99 (unpublished manuscript name) Ph.D. Thesis, University of California at Berkeley, Berkeley, California. 605 p.

Type Series. — Holotype, vivip. apt.; on slide with 1 paratype vivip. apt., holotype at bottom (6 o'clock position) and mounted inverted; data: CALIFORNIA. *PLUMAS Co.:* jct hwys 36 & 89, 1340 m, 19 Jul 1977, J. T. Sorensen (77G23), *Pinus jeffreyi.* Holotype deposited in The Natural History Museum, London. Paratypes (all same data as holotype): 8 vivip. apt. on 6 slides including holotype slide; 4 paratype slides with 1 adult vivip. apt. and 1 nymph, only the adults are paratypes. Paratype slides deposited: 1 slide in NMNH, Washington, D.C.; 1 slide in CNC, Ottawa, Ontario; 3 slides in Sorensen collection.

Viviparous Apterae. — Morphology: Body length: 2.10–2.64 (2.29 ± 0.14) mm. HEAD: Primary rhinarium on terminal antennal segment (V) not exceptionally distad, distance from tip of processus terminalis to distal face of rhinarial rim greater than $0.5\times$ diameter of rhinarium; distal face of rhinarial rim usually oblique to longitudinal axis of antennal segment; rhinarial membrane not conspicuously protuberant. Length of antennal segment V: 113–145 (132 ± 8) μ, processus terminalis: 35–45 (38 ± 3) μ; IV: 90–139 (116 ± 16) μ; III: 183–230 (201 ± 13) μ; II: 83–90 (87 ± 2) μ. Length of longest setae on frons: 48–88 (71 ± 10) μ, tips incrassate to sharp. Head width: 265–357 (329 ± 20) μ. Length of stylets: 622–969 (821 ± 81) μ; ultimate rostral segment: 88–108 (101 ± 5) μ, rostral tip reaching abdominal terga I–II in dorsal view through slide-mounted specimens. Head + pronotum fused, total length: 428–500 (470 ± 20) μ. THORAX: Meso + metanota fused, total length: 400–510 (446 ± 32) μ. ABDOMEN: Tergum I free, length: 158–204 (183 ± 14) μ; terga II–VII fused, VIII free. Maximum distal width of flange on siphunculi: 40–60 (49 ± 5) μ; siphunculi truncated conical, protruding 0.3–$0.6\times$ maximal distal width. Ventral abdominal sclerites on segments III–IV subquadrate to sublinear, often centrally constricted; moderate to large, length: 50–90 (67 ± 11) μ, 1.2–$2.3\times$ diameter of metatibiae. Dorsal (major + minor) setae (see Fig. 1C) on abdominal terga III–IV: 8–11 (10 ± 1), tips sharp, in 2 rows with regular positions, lateral-most minor dorsal seta in anterad row; marginal setae 4–6 each side. Setae on abdominal tergum VIII: 8–11 (9 ± 1), length: 55–98 (70 ± 12) μ, tips incrassate to sharp, in 1–2 rows. Cauda broadly rounded; caudal protuberance absent to poorly developed; length of longest caudal setae: 93–130 (108 ± 12) μ, tips sharp. LEGS: Length of meta-

femora: 836–1142 (948 ± 87) μ; metatibiae: 1061–1561 (1276 ± 130) μ; longest dorsal setae on central one-third of metatibiae: 60–113 (92 ± 16) μ, 1.5–2.8× diameter of metatibiae, tips blunt to sharp; approximately equal or very gradually increasing distally, no setal length dimorphism; longest ventral setae on metatibiae: 33–68 (49 ± 10) μ, tips sharp. Length of metabasitarsus: 140–200 (168 ± 15) μ; metadistitarsus: 208–275 (240 ± 22) μ. Ratio of metadistitarsus to metabasitarsus less than 1.9:1, mean 1.43:1. *Pigmentation:* Color in life: Body straw yellow, frequently with dark spots; head concolorous to orange-brown; tibiae variable, entirely concolorous yellow, to pro- and metatibiae nearly black, mesotibiae yellow. Slide-mounted specimens: Background of body dorsum very pale to rarely light brown (usually less than 10, rarely to 30 percent pigment density), unicolorous. Terga at bases of setae on frons and dorsal (major + minor) setae on abdomen concolorous with surrounding terga, to subtly darker. Thoracic muscle attachment plates light to moderate brown, often spotted, conspicuous. Dorsal muscle attachment plates of abdomen pale to dark brown, conspicuous. Spiracular plates and ventral abdominal sclerites light to dark brown, conspicuous, rarely pale, inconspicuous. Siphunculi concolorous with surrounding terga, to subtly darker. Cauda, anal and subgenital plates pale, concolorous with abdominal tergum, to substantially darker. Antennal segments V and IV dark brown, concolorous, to V and distal one-half of IV dusky; III entirely pale to distal one-third dark brown, remainder pale; II pale; I concolorous with frons, to subtly darker. Tibiae variable, pro- and metatibiae usually uniformly light to dark brown, often nearly black, mesotibiae pale; commonly all tibiae concolorously pale. Distal four-fifths of distitarsi dusky to nearly black with tibiae.

Ultimate Stadium Nymphs of Viviparous Apterae.—Slide-mounted specimens: Nonmorphometrics as described for viviparous apterae except lacking body dorsum pigmentation suite; abdominal terga membranous with dorsal (major + minor) setae, between muscle attachment plates, arising from distinct scleroites. Mesonotum with 2 sclerotized plates extending from muscle attachment sites to engulf neighboring setal bases; plates usually distinct, faintly to darkly pigmented, diameter approximately equaling eye length.

Viviparous Alatae.—Slide-mounted specimens: Nonmorphometrics as described for viviparous apterae except lacking body dorsum pigmentation suite; abdominal terga normally membranous, dorsal (major + minor) setae between muscle attachment plates infrequently arising from distinct scleroites; antennal segments often as dark as tibiae, except proximal one-fifth of III pale. Antennal segment III with 0–2, IV with 0–1, secondary rhinaria. Epicranial suture absent. Forewing medius with single furcation arising on proximad one-third of vein; cubital base usually arising distad, infrequently proximad, on subcosta with distance between anal and cubital bases on subcosta usually relatively large, ca. 30–40 percent or more of anal vein length; usually medius, sometimes cubitus and anal veins faint, vague to absent. Abdominal terga infrequently with irregular sclerites that engulf or join muscle attachment plates and dorsal (major + minor) setal bases or scleroites.

Oviparae.—Slide-mounted specimens: Nonmorphometrics as described for viviparous apterae except abdominal terga II–VI fused, lightly to moderately sclerotic, including pleural areas, but VII and VIII free (rarely VII not free); dorsal demarcations of anterad terga not evident; siphunculi usually incorporated into sclerotic dorsum, to free; dorsal abdominal muscle attachment plates unicolorous. Pseudorhinaria on metatibiae irregular, 5–19.

Males, Fundatrices.—Unknown.

Diagnosis.—*Essigella* (*L.*) *hillerislambersi* and *E.* (*L.*) *fusca* are difficult to distinguish. Darker individuals of both can be separated from other *Essigella,* except *E.* (*L.*) *eastopi,* by their tibial pigmentation suite [see *E.* (*L.*) *eastopi* diagnosis]. Dark *E.* (*L.*) *hillerislambersi* usually have a paler background on the body dorsum than, and lack the developed body dorsum pigmentation of, *E.* (*L.*) *eastopi.* All three *Lambersella* species grade into completely pale individuals that can be differentiated from other pale *Essigella* by the diagnostics given for *E.* (*L.*) *eastopi.* Although *E.* (*L.*) *hillerislambersi* is a larger species, with an often longer antennal segment III, than either *E.* (*L.*) *fusca* or *E.* (*L.*) *eastopi,* overlapping morphometric variation in these species requires that reliable separation use the discriminant function in the key to the viviparous apterae [couplet 20].

Range.—California, southwestern Oregon, extreme western Nevada (Fig. 4B).

Hosts.—*Pinus jeffreyi* Greville & Balfour; a single occurrence on *P. attenuata*

Lemmon is a questionable host determination; that sample (77I42), which included oviparae, was from a host tree that was very small and lacked cones, but was among mature *P. attenuata.*

Discussion.—*Essigella* (*L.*) *hillerislambersi* is the largest *Essigella,* and is a reasonable common species. It is the most multivariately divergent within the subgenus, and appears to be involved in a character displacement phenomenon with the other *E.* (*Lambersella*) taxa in sympatry. See the discussions of *E.* (*L.*) *eastopi, E.* (*L.*) *fusca fusca* and *E.* (*L.*) *fusca voegtlini* for its relationships, unrepeated here.

Coded References to This Taxon.—*Essigella* (*L.*) *hillerislambersi* has been referred to previously by: the coding "Sp. O" (Sorensen 1983 [but not section 2], 1987a, 1992b), "group A" (Sorensen 1983: section 2) and "HRL" (Sorensen 1983); and by the manuscript name *E.* "*hillerislambersi*" in Sorensen (1983).

Etymology and Common Name.—This species is named for the aphidologist Dirk Hille Ris Lambers, who served as a mentor during my early aphid taxonomy studies. Common name: Hille Ris Lambers' Jeffrey pine needle aphid.

Material Examined.—CALIFORNIA. *ALPINE Co.:* Upper Cascade Creek, E side of Ebbett's Pass on hwy 4, 5 km E of summit, 2350 m, 17 Jul 1977, JTS 77G40, *P. jeffreyi,* (apt.); W side of Monitor Pass on hwy 89, 2 km E of jct with hwy 4, 1830 m, 17 Jul 1977, JTS 77G38, *P. jeffreyi,* (apt.). *EL DORADO Co.:* Lake Tahoe, Meek's Bay, 1980 m, 16 Jul 1977, JTS 77G29, *P. jeffreyi,* (apt.); South Lake Tahoe, 1950 m, 16 Jul 1977, JTS 77G32, *P. jeffreyi,* (apt.). *INYO Co.:* jct of Lake Sabrina Rd & Southern Calif. Edison Plant 2 Rd, nr Bishop, 2130 m, 1 Aug 1977, JTS 77H4, *P. jeffreyi,* (apt.). *LOS ANGELES Co.:* 3 km SE of Big Pines on hwy 2, E of Blue Ridge Summit, 2200 m, 17 Sep 1977, JTS 77I49, *P. jeffreyi,* (apt., ovip.). *MONO Co.:* Deadman Summit on hwy 395, nr Crestview, 2440 m, 31 Jul 1977, JTS 77G72, *P. jeffreyi,* (apt., alat.); E side of Monitor Pass on hwy 89, 2070 m, 17 Jul 1977, JTS 77G37, *P. jeffreyi,* (apt.). *NEVADA Co.:* Prosser Lake Recreation Area, hwy 89, 25 Jun 1977, JTS 77F5, *P. jeffreyi,* (apt.). *PLUMAS Co.:* hwy 36, 8 km W of jct with hwy 89, 1460 m, 10 Jul 1977, JTS 77G25, *P. jeffreyi,* (apt.); (type series) jct of hwys 36 & 89, 1340 m, 10 Jul 1977, JTS 77G23, *P. jeffreyi,* (apt.). *RIVERSIDE Co.:* 2 km N of Paradise Valley on hwy 74, 1500 m, 9 Sep 1977, JTS 77I18, *P. jeffreyi,* (apt.). *SAN BERNARDINO Co.:* San Bernardino Natl Forest, Heart Bar, 30 Aug 1972, D. J. Voegtlin, DJV 73, *P. jeffreyi,* (apt.); same but Keller Peak Cmpgd, 2200 m, 17 Sep 1977, JTS 77I42, *P. attenuata,* (apt., ovip.); same but JTS 77I41, *P. jeffreyi,* (apt., ovip.); San Bernardino Mts, 2 km S of jct of hwy 38 & Jenks Lake Rd, 2200 m, 16 Sep 1977, JTS 77I39, *P. jeffreyi,* (apt.). *SAN DIEGO Co.:* Pioneer Mail Trail Picnic Area, Cleveland Natl Forest, 3 km N of Mt Laguna on hwy S1, 1740 m, 12 Sep 1977, JTS 77I31, *P. jeffreyi,* (apt.). *SIERRA Co.:* 18 km S of Sierraville on hwy 89, 26 Jun 1977, JTS 77F7, *P. jeffreyi,* (apt.). *TEHAMA Co.:* 5 km E of Childs Meadows on hwy 89, 1460 m, 10 Jul 1977, JTS 77G21, *P. jeffreyi,* (apt.). *TULARE Co.:* E of Big Meadows Cmpgd, Sierra Natl Forest, 2320 m, 13 Aug 1977, JTS 77H13, *P. jeffreyi,* (apt., alat.). *TUOLUMNE Co.:* Yosemite Natl Park, nr Porcupine Flat-Porcupine Creek, 2500 m, 30 Jul 1977, JTS 77G67, *P. jeffreyi,* (apt., alat.). *VENTURA Co.:* Mt Pinos Summit, 2680 m, 18 Sep 1977, JTS 77I55, *P. jeffreyi,* (apt.); Reyes Peak Rd, 10 km E of Pine Summit of hwy 33, 2200 m, 19 Sep 1977, JTS 77I59, *P. jeffreyi,* (apt.). *COUNTY UNCERTAIN:* Eagle Peak, Stanislaus Natl Forest, 8 Jul 1979, D. J. Voegtlin, DJV 558, *P. jeffreyi,* (apt.); Lake Tahoe, 17 Jul 1969, R. Luck, *P. jeffreyi,* (apt.). NEVADA. *ORMSBY Co.:* E side of Spooner Summit on hwy 50, 1770 m, 16 Jul 1977, JTS 77G33, *P. jeffreyi,* (apt.).

ESSIGELLA (*ESSIGELLA*) DEL GUERCIO, 1909, NEW STATUS

Lachnus Burmeister, 1835 (in part), Handbuch der Entomologie, Berlin, 2: 91 (genus attributed to Illiger); Essig, 1909, Pomona J. Entomol., 1: 1–4.

"*Essigella* (*Essigella*)" Sorensen, 1983: 73 (unpublished manuscript name) Ph.D. Thesis, University of California at Berkeley, Berkeley, California. 605 p.

Type Species.—*Lachnus californicus* Essig, 1909, Pomona J. Entomol., 1: 1–4.

Viviparous Apterae.—*Morphology:* Body relatively broad to narrow. Meso- and metanota fused dorsally; abdominal tergum I usually free but may be fused with meso + metanota, especially laterally. Dorsal setae (majors and minors) between muscle attachment plates on abdominal segments III–IV in 1 rarely irregular row with mesad (spinal) setae occasionally slightly anterad or posterad of others (see Figs. 1E–F); lateral-most dorsal minor seta on each side not anterad (very rarely so) of the immediately mesad neighbor. Abdominal terga III–IV each with 5–10, rarely to 12, dorsal (major + minor) and 2–5 (per side) marginal setae; tergum VIII with usually 6, frequently to 8, rarely to 10, setae. Longest dorsal seta on central one-third of metatibiae to nearly 4× tibial diameter, tips incrassate to sharp; these setae not dimorphic in length but sometimes exceptionally variable among specimens, with nearly equal length, or gradually increasing, along metatibiae. Ventral abdominal sclerites on segments III–IV reduced (rudimentary), irregular stellate to large, subquadrate, subcircular or subelliptical. Species means for length ratio of metadistitarsus to metabasitarsus varying between 1.47:1 to 1.69:1. *Pigmentation:* Body dorsum variable, pale to nearly black, unicolorous or variable, but not strongly mottled; bases of dorsal setae of abdomen concolorous with surrounding terga to substantially darker. Tibiae varying from entirely pale to nearly black; when darkened, all concolorous or pro- and mesotibiae paler than metatibiae.

Diagnosis.—See the key to the subgenera of *Essigella.*

Discussion.—This clade has ecologically transferred to diploxylon pines of the subgenus *Pinus* (Sorensen 1987a). The transfer is exclusive of subsection Ponderosae pines, although *E. (E.) californica*, which is relatively polyphagous within *Pinus*, feeds on that subsection also. Some *E. (Essigella)* taxa have moved to Pinaceace hosts other than *Pinus* [i.e., *E. (E.) wilsoni*, *E. (E.) alyeska*]. Some have partially reinvaded haploxylon pines in the subgenus *Strobus*, through their relatively polyphagous feeding habits [i.e., *E. (E.) californica*, *E. (E.) pini*]. Others [i.e., *E. (E.) hoerneri*] have entirely reinvaded subgenus *Strobus*, in the unoccupied niches of section Parrya subsection Cembroides. Sorensen (1983) examined the relationships among the *E. (Essigella)* species with discriminant function and principal component analyses, using morphometric data, and with principal coordinate analysis, multidimensional scaling and various UPGMA and single-linkage clustering algorithms, using coded quantitative and qualitative data.

The phylogenetic analyses here indicate that *Essigella (Essigella)* can be divided into two series with historical biogeographic relevance: series A, which contains *E. (E.) californica*, *E. (E.) essigi*, *E. (E.) hoerneri*, *E. (E.) pini*, and *E. (E.) wilsoni*; and series B, which contains *E. (E.) alyeska*, *E. (E.) critchfieldi*, *E. (E.) knowltoni braggi*, and *E. (E.) knowltoni knowltoni*. Series A is paraphyletic, and shares hosts suspected of having an austral origin during the Tertiary [i.e., Madro-Tertiary geoflora] (Axelrod 1958, 1967; Raven & Axelrod 1978). *Essigella (E.) californica*, and *E. (E.) hoerneri*, however, clearly form a monophyletic species group within this series. *Essigella (E.) essigi* is the least derived species in the subgenus, and its immediate ancestral node (Fig. 13: node 7) on the phylogenetic tree is shared by all other *E. (Essigella)*, making it the functional sister-group for the remainder of the subgenus.

Series B is monophyletic, with a synapomorphy as a relatively broad head width [see discussion of *E. (E.) alyeska*]. Members of Series B occur on *Pinus contorta* Douglass ex Loudon, *Pinus banksiana* Lambert and *Picea glauca* (Moench) Voss; hosts that have relatively northern distributions in North America (Critchfield & Little 1966, Little 1971), and are of boreal origin during the Tertiary [i.e., Arcto-Tertiary geoflora]. Sorensen (1992a) has analyzed the biological groupings and host associations within the *E. (E.) knowltoni* complex, and has found its species, subspecies and populations to closely overlay the geographic and terpene variance

in *Pinus contorta* and its subspecies [see the discussions under *E.* (*E.*) *critchfieldi* and *E.* (*E.*) *knowltoni*]. He also notes the presence of character displacement in both qualitative and multivariate quantitative traits among the taxa in this species group.

Note that Sorensen (1983) reversed the letters for series A and B, as manuscript references; in that unpublished work, series A and B were paraphyletic and monophyletic groups, respectively.

Coded References to This Taxon. —Sorensen (1983) referred to this taxon under the manuscript name "*Essigella* (*Essigella*)." Sorensen (1987a) referred to the assemblage that comprise this taxon as group "III" or, with reference to its sub-components, as "I-H-B-A-C-D-E-F-G" [or *entire* permutations therefore]; in Sorensen (1992b), the latter refers to it.

Material Examined. —*Essigella* (*E.*) *alyeska, E.* (*E.*) *californica, E.* (*E.*) *critchfieldi, E.* (*E.*) *essigi, E.* (*E.*) *hoerneri, E.* (*E.*) *knowltoni braggi, E.* (*E.*) *knowltoni knowltoni, E.* (*E.*) *pini, E.* (*E.*) *wilsoni.*

Series A

Essigella (*Essigella*) *essigi* Hottes, 1957

Essigella essigi Hottes, 1957: 84, Proc. Biol. Soc. Wash., 70: 84–85.

Primary Type. —Holotype, vivip. alat., on slide with 5 other alat. and 7 apt., holotype shown by arrow (near center position among all specimens, 9 o'clock among alat.); slide data: "*Pinus radiata,* Redwood City, California, June 10, 1939, L. Blanc/Paratype, *Essigella* holotype *essigi* F. C. Hottes, Essig." (Redwood City is in San Mateo Co.). Holotype deposited in the Essig Museum of Entomology, University of California at Berkeley, Berkeley, California.

Viviparous Apterae. —*Morphology:* Body length: 1.33–1.93 (1.62 ± 0.18) mm. HEAD: Primary rhinarium on terminal antennal segment (V) not exceptionally distad, distance from tip of processus terminalis to distal face of rhinarial rim greater than 0.5× diameter of rhinarium; distal face of rhinarial rim usually oblique to longitudinal axis of antennal segment; rhinarial membrane not conspicuously protuberant. Length of antennal segment V: 90–125 (109 ± 11) μ, processus terminalis: 23–43 (36 ± 5) μ; IV: 60–93 (78 ± 10) μ; III: 110–153 (133 ± 14) μ; II: 56–68 (63 ± 4) μ. Length of longest setae on frons: 13–65 (29 ± 13) μ, tips incrassate. Head width: 228–275 (249 ± 13) μ. Length of stylets: 541–755 (621 ± 56) μ; ultimate rostral segment: 50–78 (63 ± 7) μ, rostral tip reaching abdominal terga I–III in dorsal view through slide-mounted specimens. Head + pronotum fused, total length: 245–388 (324 ± 39) μ. THORAX: Meso + metanota fused, combined total length when dorsally demarcated from abdominal tergum I: 250–377 (312 ± 36) μ. ABDOMEN: Tergum I fused with metanotum, completely so across dorsum (pale individuals) to fused laterally only (dark individuals), length when dorsally demarcated: 92–143 (123 ± 19) μ; terga II–VII fused, VIII free. Maximum distal width of flange on siphunculi: 15–29 (21 ± 4) μ; siphunculi flush with tergum. Ventral abdominal sclerites on segments III–IV subquadrate, subcircular to subelliptical; length: 35–60 (50 ± 7) μ, 1.1–2.0× diameter of metatibiae. Dorsal (major + minor) setae (see Fig. 1E) on abdominal terga III–IV: 8, very rarely 7 or 9, tips sharp, in 1 row, infrequently with mesad pair of setae posterad; marginal setae 3, infrequently 2, per segment each side. Setae on abdominal tergum VIII: 6 to rarely 8, length: 5–48 (23 ± 14) μ, tips incrassate to sharp, in 1 row. Cauda rounded to broadly rounded; caudal protuberance moderately developed to nearly absent; length of longest caudal setae: 20–92 (60 ± 19) μ, tips sharp. LEGS: Length of metafemora: 367–581 (476 ± 66) μ; metatibiae: 418–694 (567 ± 87) μ; longest dorsal setae on central one-third of metatibiae: 3–43 (18 ± 11) μ, 0.1–1.3× diameter of metatibiae, tips incrassate; approximately equal or very gradually increasing distally, no setal length dimorphism; longest ventral setae on metatibiae: 5–35 (24 ± 9) μ, tips sharp. Length of metabasitarsus: 65–98 (85 ± 11) μ; metadistitarsus: 118–163 (144 ± 15) μ. Ratio of metadistitarsus to metabasitarsus less than 1.9:1, mean 1.69:1. *Pigmentation:* Color in life: Black to green throughout or green with
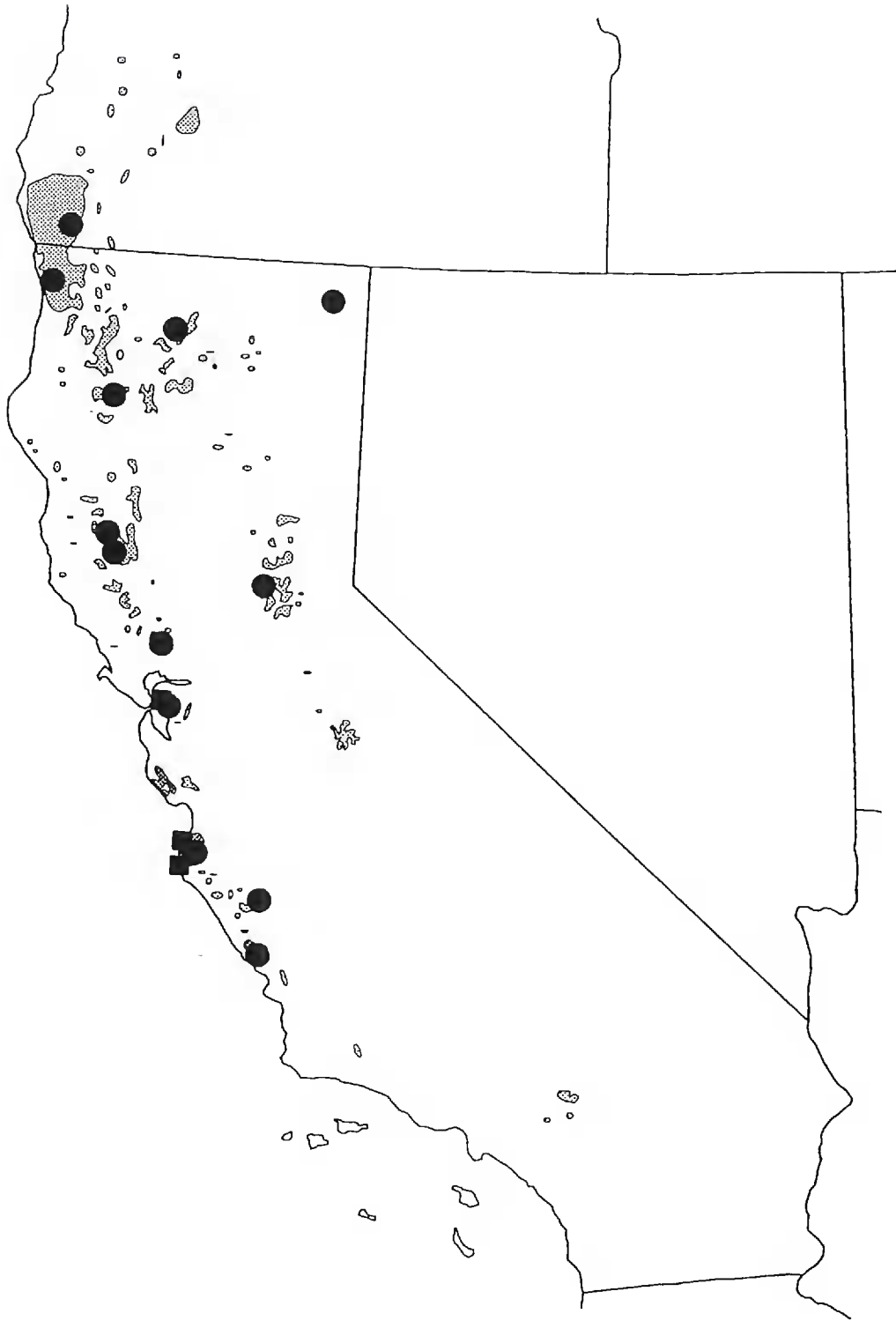
Figure 6. Distribution of *E.* (*E.*) *essigi* [dots (JTS samples), squares (nonJTS samples)], superimposed over the range of its hosts, *Pinus attenuata* [lighter shading] and *Pinus radiata* [darker shading (coastal Santa Cruz, Monterey and San Luis Obispo Counties)].

yellow-green head; frequently with dark dorsal spots when body not dark. Slide-mounted specimens: Background of body dorsum pale to dark brown or nearly black (to nearly 100 percent pigment density), unicolorous. Terga at bases of setae on frons and dorsal (major + minor) setae on abdomen concolorous with surrounding terga, to subtly darker. Thoracic muscle attachment plates and dorsal muscle attachment plates of abdomen pale, inconspicuous to dark brown, conspicuous. Spiracular plates and ventral abdominal sclerites pale to nearly black. Siphunculi concolorous with surrounding terga. Cauda, anal and subgenital plates subtly to substantially darker than abdominal terga. Antennal segments V and IV dusky to moderate brown, concolorous; III entirely pale to dusky on distal one-third, remainder pale; II concolorous with proximal III, to subtly darker; I concolorous with frons. Pro-, meso- and metatibiae concolorous, and usually equivalent to abdominal terga, sometimes subtly lighter (dark individuals), rarely darker. Distitarsi evenly moderate brown, sometimes subtly paler at proximal tip.

Ultimate Stadium Nymphs of Viviparous Apterae. — Slide-mounted specimens: Nonmorphometrics as described for viviparous apterae except lacking body dorsum pigmentation suite; abdominal terga

membranous with dorsal (major + minor) setae, between muscle attachment plates, arising from distinct scleroites; meso- and metathorax not fused. Mesonotum with 2 sclerotized plates extending from muscle attachment sites to engulf neighboring setal bases; plates usually heavily, to faintly, pigmented, diameter approximately equaling eye length.

Viviparous Alatae.—Slide-mounted specimens: Nonmorphometrics as described for viviparous apterae except lacking body dorsum pigmentation suite, and meso- and metathorax not fused; abdominal terga normally membranous, dorsal (major + minor) setae between muscle attachment plates frequently arising from distinct scleroites; antennal segments often as dark as tibiae, except proximal one-fifth of III pale. Antennal segment III with 2–3, IV with 0–1, secondary rhinaria. Epicranial suture usually strongly developed, to absent. Forewing medius usually single, infrequently single furcation arising on distad one-third of vein; cubital base usually arising distad, infrequently proximad, on subcosta with distance between anal and cubital bases on subcosta usually relatively large, ca. 30–40 percent or more of anal vein length; medius, especially cubitus and anal veins usually distinct, except infrequently proximad 10–15 percent vague. Abdominal terga infrequently with irregular sclerites that engulf or join muscle attachment plates and dorsal (major + minor) setal bases or scleroites.

Oviparae, Males, Fundatrices.—Unknown.

Diagnosis.—Adult viviparous apterae of *E.* (*E.*) *essigi* can be identified by the unique additional fusion of abdominal tergum I to fused meso + metanota. They vary from entirely pale to dark brown [like *E.* (*E.*) *critchfieldi* and some *E.* (*E.*) *knowltoni knowltoni*], and the fusion of abdominal tergum I varies inversely with pigmentation: it extends entirely across the dorsum in pale individuals, but is restricted to the lateral edges of the dorsum in dark specimens. The forewing medius of alates usually is single, or occasionally 1-branched with the furcation distad and closer to the posterad margin of the wing than to the subcosta. This alate character is similar in *E.* (*E.*) *pini* [see that diagnosis] and potentially can be confused in *E.* (*E.*) *knowltoni knowltoni* and *E.* (*E.*) *alyeska.*

Range.—California and southwestern Oregon (Fig. 6).

Hosts.—*Pinus radiata* D. Don and *P. attenuata* Lemmon, both subsection Oocarpae pines that hybridize (W. Libby, personal communication). Although *E.* (*E.*) *essigi* is commonly found on closed-cone pines, it has not been found on *P. muricata* D. Don, despite extensive collecting; its appearance on that pine would not be surprising, however. Also, one collection (77G12) exists from *P. ponderosa,* at a site about 50 mi east, by air, of the nearest stand of *P. attenuata,* near the southern Modoc-Siskiyou county border (Critchfield & Little 1966: map 58) in northwest California. Another collection (77I8) exists from *P. sabiniana,* possibly a contaminant, at the same location and immediately after a collection (77I7) from *P. attenuata.* I suspect that the locations where *E.* (*E.*) *essigi* can be found in California have probably increased substantially in recent years because of the extensive landscape planting of *Pinus radiata.*

Discussion.—*Essigella* (*E.*) *essigi* is relatively homogeneous in morphology, although specimens from southwest Oregon and the northern Californian coast tend to be very slightly more linear than those near the San Francisco Bay area and south. The autapomorphic fusion of abdominal tergum I in this species is incomplete dorsally on darker specimens, probably due to an increased sclerotization of the body dorsum; the break may be necessary for articulation (?) of the more rigid tergum on those individuals. Subtle differences between coastal populations on *P. radiata,* and inland populations on *P. attenuata* should be examined in more detail with isozyme or nucleic acid techniques.

Hottes (1957: 85) stated "I am sure that specimens of this species [*E.* (*E.*) *essigi*] were part of the original material from which Essig described *Lachnus californicus,*

although there is no actual proof in the remaining cotype material." He based this supposition on Essig's illustration (Essig 1909: fig. 2), which failed to indicate long tibial setae. Unfortunately, Hotte's reliance upon length of the dorsal setae on the tibia was entirely misguided. I have found no evidence to support his supposition.

The phylogenetic position of *E. (E.) essigi* within the subgenus is problematic. Clustering analyses on qualitative coded characters (Sorensen 1983) suggest it is probably primitive within *E. (Essigella)* because its similarities to other taxa are mostly plesiomorphies at the level of the subgenus. Ordinations on morphometric data indicate that it is close to *E. (E.) pini* and *E. (E.) wilsoni* in ordinant space; the evolutionary aspects of this are discussed in Sorensen (1992b). Cladistic analysis of coded data (unpublished data) suggest that *E. (E.) essigi* is either paraphyletically one of the more primitive *E. (Essigella)*, along with *E. (E.) pini,* or that it potentially forms a monophyletic subgroup, which is the sister-group to the remainder of the subgenus, with *E. (E.) pini.*

Intuitively, I consider *E. (E.) essigi* to be closest to *E. (E.) pini,* but I am uncertain of the exact relationship between them. Both share reduction of the alate medius to a single vein, but I am reluctant to accept the trait as a convincing, nonhomoplasious synapomorphy. I also suspect the genetic compatibility of subsection Oocarpae and Australes pines [the latter chiefly hosts *E. (E.) pini*] suggests a potentially common biogeographic origin; see the section on ecological collaboration of phylogenetic hypotheses for comments.

Coded References to This Taxon.—Essigella (E.) essigi has been referred to previously by: the coding "Sp. I" (Sorensen 1983, 1987, 1992b) and "ESSG" (Sorensen 1983), and by the name *E. essigi* in Sorensen (1983).

*Etymology and Common Name.—*Hottes (1957) apparently named this species for the aphidologist E. O. Essig, presumably because he described the first *Essigella, E. (E.) californica,* albeit as a *Lachnus.* Common name: Essig's closed-cone pine needle aphid [see etymology for *E. (E.) californica*].

*Material Examined.—*CALIFORNIA. *ALAMEDA Co.:* Berkeley, 10 Nov 1935, E. O. Essig, *P. radiata,* (apt.); same but 15 Feb 1982, J. T. Sorensen, *P. radiata,* (apt.). *DEL NORTE Co.:* 16 air km NWW of Crescent City on hwy 199, Six Rivers Natl Forest, 4 Jul 1978, JTS 78G6, *P. attenuata,* (apt., alat.). *LAKE Co.:* 21 km N of Upper Lake, Elk Mt Rd, 1030 m, 24 Jul 1977, JTS 77G60, *P. attenuata,* (apt., alat.); same but 23 km N of Upper Lake, 1160 m, JTS 77G59, (apt.); same but 26 km N of Upper Lake, JTS 77G58, (apt.). *MODOC Co.:* E side of Cedar Pass, 29 km E of Alturas, 1890 m, 3 Jul 1977, JTS 77G12, *P. ponderosa,* (apt.). *MONTEREY Co.:* 3 km N of Point Lobos State Park Reserve on hwy 1, 29 Dec 1978, JTS 78L1, *P. radiata,* (apt.); Carmel, 16 Jun 1973, D. J. Voegtlin, DJV 25, *P. radiata,* (apt.); Lockwood-San Ardo Rd, 13 km SW of jct with Paris Valley Rd, 550 m, 4 Sep 1977, JTS 77I7, *P. attenuata,* (apt.); same but JTS 77I8, *P. sabiniana,* (apt.); Monterey, 18 Jun 1973, D. J. Voegtlin, DJV 24, *P. radiata,* (apt.); same but 19 Feb 1974, T. Kono, CDFA 79B20-10-2, (apt.). *NAPA Co.:* 3 km N of Angwin, Howell Mt Rd, 4 Feb 1978, JTS 79B2, *P. attenuata,* (apt.). *PLACER Co.:* 6 km W of Dutch Flat on hwy 80, 2 Aug 1978, JTS 78H2, *P. attenuata,* (apt.). *SAN LUIS OBISPO Co.:* Cambria Pines, 5 Sep 1977, JTS 77I12, *P. radiata,* (apt.). *SAN MATEO Co.:* (paratype) Redwood City, 10 Jun 1939, L. Blanc, *P. radiata,* (apt., alat.). *SANTA CLARA Co.:* (paratype) Palo Alto, Stanford Univ., 30 Mar 1938, E. O. Essig, *P. radiata,* (apt.,); (paratype) same but 25 Apr 1930, P.S.B., (apt.); Morgan Hill, 14 Oct 1942, Bell, CDFA 42J10, *P. attenuata,* (apt.). *SISKIYOU Co.:* Snowman Hill Summit on hwy 89, 8 km E of jct with hwy 5, 1360 m, 2 Jul 1977, JTS 77G3, *P. attenuata,* (apt.). *TRINITY Co.:* Junction City, 11 km of Weaverville on hwy 299, 430 m, 20 Aug 1977, JTS 77H23, *P. attenuata,* (apt.). OREGON. *JOSEPHINE Co.:* 2 km N of O'brien on hwy 199, 4 Jul 1978, JTS 78G11, *P. attenuata,* (apt.).

Essigella (Essigella) pini Wilson, 1919

Essigella pini Wilson, 1919: 2, Entomol. News, 30: 2–3.
Essigella patchae Hottes, 1957: 98, Proc. Biol. Soc. Wash., 70: 98–100. NEW
  SYNONYM.

Primary Type.—Lectotype, vivip. alat., on slide alone; data: "(Lectotype)/82-
14/11, *Essigella pini* Wilson, Cotype, *Pinus virginiana,* Plummer's Is., Md., May
27, 1914." Lectotype deposited in the Granovsky Collection, Department of
Entomology, Fisheries & Wildlife, University of Minnesota, St. Paul, Minnesota.

Hottes (1957: 103) designated a vivip. alat., from the Granovsky collection as
lectotype. A slide that is so labeled does exist, although I doubt that Hottes
personally labeled it because the printing does not match his, and he did not label
other lectotypes in this genus; I have seen this specimen and consider it the
lectotype.

Viviparous Apterae.—*Morphology:* Body length: 1.57–2.03 (1.79 ± 0.15) mm. HEAD: Primary
rhinarium on terminal antennal segment (V) not exceptionally distad, distance from tip of processus
terminalis to distal face of rhinarial rim greater than 0.5× diameter of rhinarium; distal face of rhinarial
rim usually oblique to longitudinal axis of antennal segment; rhinarial membrane not conspicuously
protuberant. Length of antennal segment V: 98–133 (115 ± 9) μ, processus terminalis: 25–38 (31 ±
4) μ; IV: 73–100 (84 ± 8) μ; III: 110–158 (136 ± 16) μ; II: 63–79 (68 ± 4) μ. Length of longest setae
on frons: 15–73 (29 ± 16) μ, tips incrassate. Head width: 245–316 (276 ± 19) μ. Length of stylets:
541–663 (572 ± 34) μ; ultimate rostral segment: 55–75 (67 ± 5) μ, rostral tip reaching abdominal
terga I–II in dorsal view through slide-mounted specimens. Head + pronotum fused, total length:
326–454 (400 ± 36) μ. THORAX: Meso + metanota fused, total length: 265–367 (327 ± 33) μ.
ABDOMEN: Tergum I free, length: 112–163 (134 ± 15) μ; terga II–VII fused, VIII free. Maximum
distal width of flange on siphunculi: 15–35 (28 ± 5) μ; siphunculi usually flush to slightly protruding
to 0.3× maximal distal width. Ventral abdominal sclerites on segments III–IV usually subcircular,
subquadrate to subelliptical, sometimes irregular, asterisk-shaped, or constricted anteriorly; length:
40–75 (54 ± 8) μ, 1.0–2.0× diameter of metatibiae. Dorsal (major + minor) setae (see Fig. 1F) on
abdominal terga III–IV: 6, infrequently 7, tips sharp, in 1 row; marginal setae 2 per segment, each
side. Setae on abdominal tergum VIII: 6, length: 8–25 (13 ± 5) μ, tips incrassate to sharp, in 1 row.
Cauda rounded; caudal protuberance well developed, often pointed, to moderately developed; length
of longest caudal setae: 43–120 (75 ± 20) μ, tips sharp. LEGS: Length of metafemora: 398–581 (486
± 57) μ; metatibiae: 561–831 (675 ± 79) μ; longest dorsal setae on central one-third of metatibiae:
11–33 (17 ± 6) μ, 0.3–1.0× diameter of metatibiae, tips usually incrassate, infrequently sharp; ap-
proximately equal or very gradually increasing distally, no setal length dimorphism; longest ventral
setae on metatibiae: 23–68 (35 ± 11) μ, tips sharp. Length of metabasitarsus: 79–103 (89 ± 6) μ;
metadistitarsus: 138–163 (147 ± 9) μ. Ratio of metadistitarsus to metabasitarsus less than 1.9:1, mean
1.65:1. *Pigmentation:* Color in life: Green with yellow-orange to red-orange head (from notes on C.
F. Smith slides). Slide-mounted specimens: Background of body dorsum pale (to 10 percent pigment
density), unicolorous. Terga at bases of setae on frons and dorsal (major + minor) setae on abdomen
concolorous with surrounding terga. Thoracic muscle attachment plates and dorsal muscle attachment
plates of abdomen pale, inconspicuous. Spiracular plates and ventral abdominal sclerites pale, to
moderate brown, conspicuous. Siphunculi concolorous with surrounding terga. Cauda, anal and subgenital
plates pale, concolorous with, to subtly dusky and slightly darker than abdominal terga. Antennal
segments V and IV pale to light brown, concolorous; III entirely pale to distal one-third concolorous
with V and IV; II concolorous with proximal III; I concolorous with frons. Pro-, meso- and metatibiae
usually pale, concolorous and equivalent to body dorsum, infrequently entire tibiae slightly dusky,
subtly darker than dorsum. Distitarsi entirely pale to subtly dusky on distal one-third.

Ultimate Stadium Nymphs of Viviparous Apterae.—Slide-mounted specimens: Nonmorphometrics
as described for viviparous apterae except lacking body dorsum pigmentation suite; abdominal terga
membranous with dorsal (major + minor) setae, between muscle attachment plates, arising from
distinct scleroites. Mesonotum with, very rarely lacking, 2 sclerotized plates extending from muscle

attachment sites to engulf neighboring setal bases; plates faintly to heavily pigmented, diameter approximately equaling eye length.

Viviparous Alatae. —Slide-mounted specimens: Nonmorphometrics as described for viviparous apterae except lacking body dorsum pigmentation suite; abdominal terga normally membranous, dorsal (major + minor) setae between muscle attachment plates occasionally arising from distinct scleroites; antennal segments often as dark as tibiae, except proximal one-fifth of III pale. Antennal segment III with 2–3, IV with 0, secondary rhinaria. Epicranial suture vaguely to strongly developed. Forewing medius usually single, infrequently single furcation arising on distad one-third of vein; cubital base usually arising distad on subcosta with distance between anal and cubital bases on subcosta usually relatively large, ca. 30–40 percent or more of anal vein length; medius, especially cubitus and anal veins distinct, except infrequently proximad 10–15 percent vague. Abdominal terga infrequently with irregular sclerites that engulf or join muscle attachment plates and dorsal (major + minor) setal bases or scleroites.

Oviparae. —Slide-mounted specimens: Nonmorphometrics as described for viviparous apterae, abdominal terga II–VII fused, moderately sclerotic, including pleural areas, tergum VIII free (uncommonly tergum VII free, demarcations of II–VI evident laterally); dorsal demarcations of anterad terga sometimes evident; siphunculi incorporated into sclerotic field, to free; dorsal abdominal muscle attachment plates unicolorous. Pseudorhinaria on metatibiae irregular, 8–15.

Males, Fundatrices. —Unknown.

Diagnosis. —This species is pale and may be confused with other pale *Essigella*; it requires the combination of several characters for identification. *Essigella* (*E.*) *pini* can be separated from all *Essigella*, except *E.* (*E.*) *californica* and *E.* (*E.*) *hoerneri*, by having six (Fig. 1F), instead or eight or more, dorsal (major + minor) setae on abdominal terga III–IV. It differs from *E.* (*E.*) *californica* and *E.* (*E.*) *hoerneri* by having usually large subcircular-subquadrate, rather than usually small irregular, ventral abdominal sclerites on abdominal segments III–IV, and by having usually large invasive, instead of small noninvasive, mesonotal muscle attachment plates on later stadia nymphs of apterae. The mean lengths of antennal segments III and the metatibiae are shorter, but overlapping, in proportion to body length in *E.* (*E.*) *pini* than in either *E.* (*E.*) *californica* or *E.* (*E.*) *hoerneri*. The caudal protuberance of *E.* (*E.*) *pini* also is often abnormally long and pointed, but the trait is not an entirely satisfactory discriminator. Alates of *E.* (*E.*) *pini* differ from other species, except *E.* (*E.*) *essigi*, in having the medius usually single, or infrequently 1-branched with the furcation exceptionally distad; but *E.* (*E.*) *knowltoni knowltoni* has also rarely shown this condition. Although the relative stability of the trend to a single medius for *E.* (*E.*) *pini* and *E.* (*E.*) *essigi* seems a reasonable partial diagnostic for those species, unknown alate morphs and interspecific variance in several *Essigella* species make discriminatory use of venation potentially questionable.

Synonyms. —*Essigella patchae* Hottes, NEW SYNONYM: holotype, vivip. alat., as a single fragmented specimen on the slide; data: MAINE. *PENOBSCOT Co.:* Stillwater, 4 Jul 1909, *Pinus strobus* L. *Essigella patchae* holotype deposited in the NMNH.

Range. —Eastern U.S.; one record from southern Quebec (Fig. 7).

Hosts. —Notably *Pinus virginiana* P. Miller, *P. taeda* L., *P. strobus* L.; presumably many species of *Pinus* subsection Australes; subsection Sylvestres pines also recorded as hosts. Note that because *E.* (*E.*) *pini* is the only *Essigella* that I have not personally collected, during extensive sampling of the western Nearctic (Sorensen 1983), I cannot attest to the accuracy of determination of its hosts, as with other *Essigella*. Indeed, because the aphid occurs only in the eastern U.S., and it
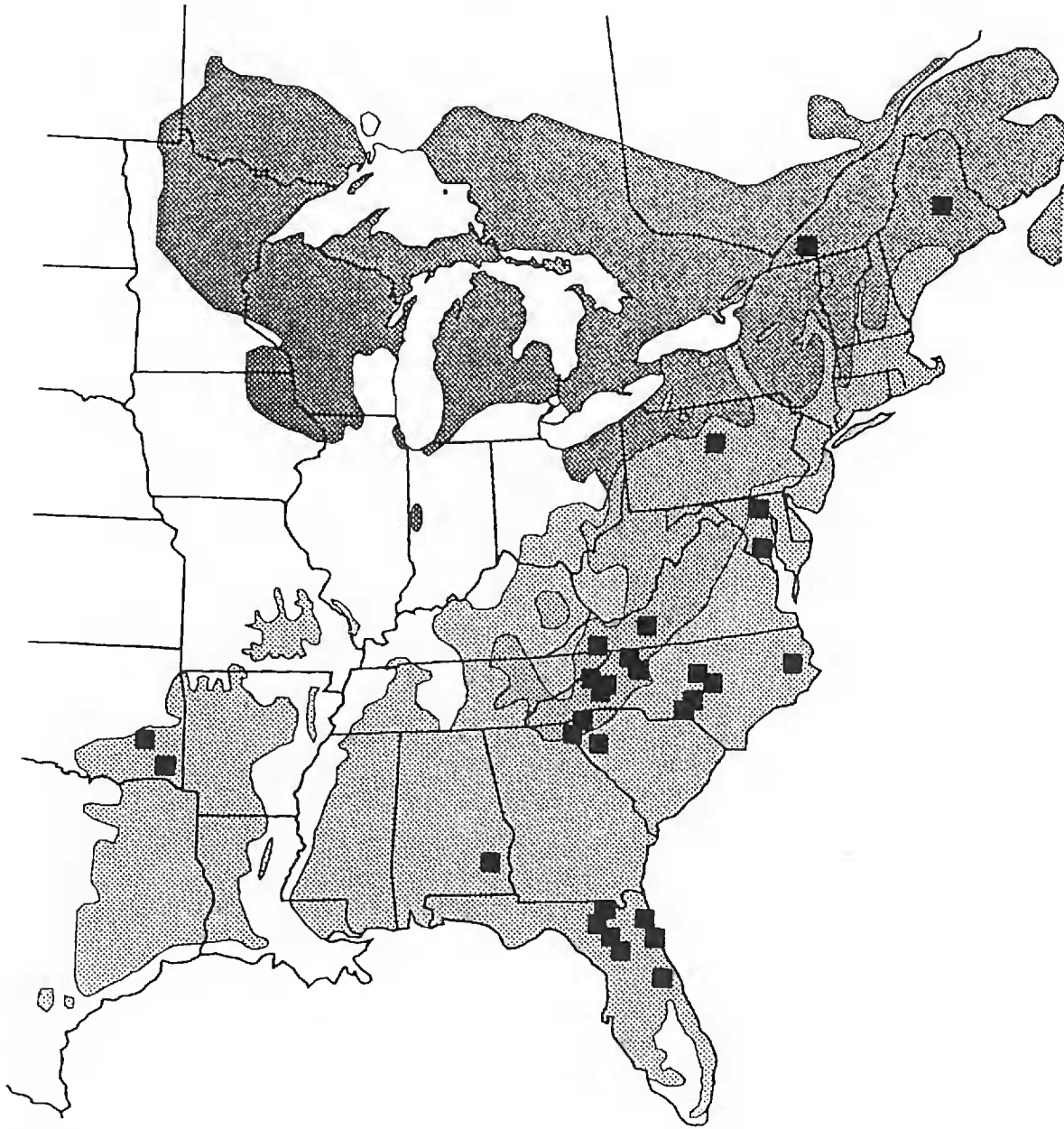
Figure 7.   Distribution of *E.* (*E.*) *pini* [squares (nonJTS samples)], superimposed over the ranges of its hosts, *Pinus strobus* [darker + moderate shading] and an amalgamation of subsection Australes plus eastern subsection Contortae pines [lighter + moderate shading] (moderate shading indicates the distributional overlap of hosts).

could not often be successfully identified until now (see discussion), many western pine species attributed as its hosts are in error.

Discussion.—*Essigella* (*E.*) *pini,* known from the eastern Nearctic only, has been the most confused *Essigella* with regard to misidentifications. This is, no doubt, due in large part to Hottes' (1957) erroneous key. Using that key, it is conceivable that at least some individuals (albeit, small and pale in several instances) of all species, except *E.* (*L.*) *hillerislambersi,* might key out to Hottes' "*E. pini.*"

References to *Essigella* "*pini*" from the western U.S. and Canada (i.e., Knowlton 1930, Gillette & Palmer 1931, Palmer 1952, Smith & Parron 1978) are in error and clearly do not represent that species. I cannot determine exactly to what they correctly refer, because adequate diagnostics are not mentioned. Such references evoke potential confusion with *E.* (*E.*) *californica, E.* (*E.*) *hoerneri, E.* (*E.*) *wilsoni, E.* (*L.*) *fusca fusca, E.* (*E.*) *knowltoni knowltoni* and *E.* (*A.*) *kirki,* due to the geography involved and the earlier erroneous diagnostic fixation on the length of the dorsal setae of the metatibiae. A single alate from Quebec, captured in a

Malaise trap (F. W. Quednau, personal communication), appears to be the only Canadian record of this species. Patti & Fox (1981a, b) discuss the seasonal occurrence and intratree distribution of *E. (E.) pini* in South Carolina.

Essigella (E.) pini appears to be relatively homogeneous morphologically. Because it was not extensively sampled over its range during this study, however, knowledge of its variation is drawn only from collections by others, which have relatively limited geographic spread and continuity. It shows infrequent variability in reduction of the ventral abdominal sclerites on segments III–IV, but this trait is paralleled within other species.

Placement of *E. (E.) pini* within the subgenus was confusing during analysis; for comments, see the discussion of *E. (E.) essigi*. It shows several qualitative loss-reduction apomorphies that are considered to be homoplasious with *E. (E.) californica* and *E. (E.) hoerneri*, and a few others with *E. (E.) wilsoni* and *E. (E.) alyeska*. The fusion of abdominal terga on its oviparae is also problematic [see character discussion section].

Coded References to This Taxon.—*Essigella (E.) pini* has been referred to previously by: the coding "Sp. H" (Sorensen 1983, 1987a, 1992b) and "PINI" (Sorensen 1983), and by the name *E. pini* in Sorensen (1983).

Etymology and Common Name.—Wilson (1919) presumably named this species with reference to the host genus, *Pinus*. Common name: the eastern pine needle aphid; although Palmer (1952: 16) refers to this species as "The Speckled Pine Needle Aphid," the common name indicated here is more appropriate and less confusing because many *Essigella* are speckled.

Material Examined.—ALABAMA. *BARBOUR Co.:* Eufaula, 10 Feb 1876, *Pinus* sp., (apt.). FLORIDA. *ALACHUA Co.:* Gainesville, 23 Mar 1928, A. Tissot, ANT F323-28, *P. taeda,* (apt., alat.); same but no date, ANT F886-32, (apt., alat.). *COLUMBIA Co.:* 22 Mar 1973, G. Hertel, *P. elliottii* Engelmann, (apt.); 26 May 1972, G. Hertel, *P. elliottii,* (alat.). *SAINT JOHNS Co.:* St. Augustine, 10 May 1945, D. & B. Darry, *P. taeda,* (apt.); same but 24 May 1945, D. & B. Darry, (alat.). *SEMINOLE Co.:* Sanford, 23 Feb 1929, A. Tissot, ANT F480-29, *P. taeda,* (alat.). MAINE. *PENOBSCOT Co.:* Stillwater, 4 Jul 1909, E. M. Patch, MAES 46-09, *P. strobus,* (alat.). MARYLAND. *BALTIMORE Co.:* Sheppard Pratt, 3 Aug 1974, A. Scarbough, (alat.). *PRINCE GEORGES Co.:* Beltsville, 19 Jun 1978, W of Cantelo, yellow pan trap, (alat.). *COUNTY UNCERTAIN:* (lectoype) Plummer's Island, 27 Apr 1914, *P. virginiana,* (apt., alat.). NORTH CAROLINA. *ALLEGANY Co.:* Gladesville, 17 Jun 1959, D. A. Young, *Pinus* sp., (apt.). *BANCOMBE Co.:* Twin Tunnels, (Blue Ridge) Parkway, 29 Jul 1958, C. F. Smith, CFS 58-347, *Pinus* sp., (apt.). *CHEROKEE Co.:* N of Andrews, 24 Jul 1958, C. F. Smith, CFS 58-309, *Pinus* sp., (apt., alat.). *DURHAM Co.:* Durham, 10 Jan 1978, D. Whitman, *P. lambertiana,* (apt.); same but 22 Oct 1959, S.S.T., *P. taeda,* (apt.); same but 8 Jan 1979, J. Richmond, (apt.). *MACON Co.:* Highlands, Mt Satulah, 29 Sep 1970, C. F. Smith C. S. Smith & C. Sullivan, *P. rigida* P. Miller (alat.). *MOORE Co.:* West End, 30 Oct 1958, S.S.T., *Pinus* sp., (apt., alat.). *RICHMOND Co.:* Norman, 30 Oct 1958, S.S.T., *Pinus* sp., (apt.). *WAKE Co.:* McCullers, 18 May 1967, C. F. Smith, CFS 67-28b, *P. taeda,* (apt.); Umstead Park, 30 May 1960, C. F. Smith, CFS 60-303, *P. taeda,* (apt., alat.). *WASHINGTON Co.:* Roper, 10 Feb 1975, C. G. Livingston, *P. taeda,* (apt.). *WILKES Co.:* McGrady, 14 Oct 1963, C. F. & C. S. Smith, CFS 63-166, (alat.). *YANCEY Co.:* 2.4 km (1.5 mi) E of Mt Mitchell State Park entrance, 23 Jul 1970, G. Fedde, *P. pungens* Lambert (apt., alat.). Crabtree Meadows, (Blue Ridge) Parkway, 12 Oct 1958, S.O.T., *P. strobus,* (apt., ovip.); same but *Pinus* sp., (apt.). OKLAHOMA. *LATIMER Co.:* Robber's Cave State Park, 19 Sep 1957, Van Cleave, *P. echinata* P. Miller (apt., alat.). *McCURTAIN Co.:* Broken Bow, 13 Sep 1960, Van Cleave, *P. echinata,* (apt.). PENNSYLVANIA. *CENTRE Co.:* State College, 3 Oct 1959, J. Pepper, *P. sylvestris* L., *P. resinosa* Aiton, *P. strobus,* (apt., alat.). SOUTH CAROLINA. *OCONEE Co.:* Seneca, 26 May 1962, R. Eikenbarry, *Pinus* sp., (apt.). *PICKENS Co.:* Clemson, 4 Apr 1973, K. Griffith, *Pinus* sp., (apt., alat.); same but 6 Jun 1977, W of Hood, *P. taeda,* (alat.). VIRGINIA. *MONTGOMERY Co.:* Blacksburg, 6 Feb 1967, W. A. Allen, *P. taeda,* (apt.). CANADA. *QUEBEC:* Mt St. Hilaire, Cte Rouville, Meteo, 5 Jul 1979, R. Roy, Malaise trap (alat.).

Essigella (*Essigella*) *californica* (Essig), 1909

Lachnus californicus Essig, 1909: 1, Pomona J. Entomol., 1: 1–4.

Essigella californica Del Guercio, 1909: 328, Rivista di Patologia Vegetale, Anno III Num. 20–21: 328–329.

Essigella claremontiana Hottes, 1957: 79, Proc. Biol. Soc. Wash., 70: 79–81. NEW SYNONYM.

Essigella cocheta Hottes, 1957: 82, Proc. Biol. Soc. Wash., 70: 82–84. NEW SYNONYM.

Essigella monelli Hottes, 1957: 95, Proc. Biol. Soc. Wash., 70: 95–96. NEW SYNONYM.

Essigella pineti Hottes, 1957: 101, Proc. Biol. Soc. Wash., 70: 101–102. NEW SYNONYM.

Essigella swaini Hottes, 1957: 105, Proc. Biol. Soc. Wash., 70: 105–106. NEW SYNONYM.

Primary Type.—Lectotype, vivip. alat., on slide alone; data: "Monterey pine, Claremont, Cal., Feb. 14, 1909, E.O.E./type/Cotype, *Lachnus californicus* Essig, Essig/[on back] Lectotype of Hottes, J. T. Sorensen '82" (Claremont is in Los Angeles Co.). Lectotype deposited in the Essig Museum of Entomology, University of California at Berkeley, Berkeley, California.

The extent of the original type series is somewhat confused; but the [1909] series must have involved an ovipara (see discussion). The series was scattered and possibly adulterated by the addition of material collected in 1911 ("47" slides), which may be involved with Essig's (1912) redescription (see Hottes 1957: 78). Hottes (1957: 78) mentions a lectotype and describes the slide as thick, but the apparent slide merely bears a small label stating "type" below the coverslip. The label is asymmetrically placed. and could have had a prefix "lecto" removed. There are also, however, two other slides, deposited in the NMNH, bearing "type" in blue ink on the right-hand label that are part of the 1911 "47" series. I deduced what must be Hottes' lectotype based upon his description of the slide and its location, and I have labeled the slide as lectotype.

Viviparous Apterae.—*Morphology:* Body length: 1.30–2.38 (1.90 ± 0.24) mm. HEAD: Primary rhinarium on terminal antennal segment (V) not exceptionally distad, distance from tip of processus terminalis to distal face of rhinarial rim greater than 0.5 × diameter of rhinarium; distal face of rhinarial rim usually oblique to longitudinal axis of antennal segment; rhinarial membrane not conspicuously protuberant. Length of antennal segment V: 103–155 (128 ± 11) μ, processus terminalis: 30–48 (37 ± 5) μ; IV: 88–138 (109 ± 14) μ; III: 135–250 (194 ± 31) μ; II: 63–88 (77 ± 8) μ. Length of longest setae on frons: 6–73 (39 ± 18) μ, tips incrassate to sharp. Head width: 214–347 (270 ± 26) μ. Length of stylets: 551–806 (688 ± 71) μ; ultimate rostral segment: 70–98 (83 ± 8) μ, rostral tip reaching abdominal terga I–II, occasionally III, in dorsal view through slide-mounted specimens. Head + pronotum fused, total length: 316–510 (393 ± 42) μ. THORAX: Meso + metanota fused, total length: 245–571 (365 ± 57) μ. ABDOMEN: Tergum I free, length: 82–194 (131 ± 23) μ; terga II–VII fused, VIII free. Maximum distal width of flange on siphunculi: 25–45 (36 ± 5) μ; siphunculi flush to truncated conical, protrusion to 0.7× maximal distal width. Ventral abdominal sclerites on segments III–IV usually irregular, to subcircular when small (length less than 0.6× metatibial diameter), subquadrate when large (length greater than 1.0× metatibial diameter); length: 8–63 (23 ± 14) μ, 0.3–1.1× diameter of metatibiae. Dorsal (major + minor) setae (see Fig. 1F) on abdominal terga III–IV: 6, rarely 7, tips incrassate to sharp, in 1 row; marginal setae 2 each side. Setae on abdominal tergum VIII: 6, occasionally 7, infrequently 8, length: 8–85 (36 ± 20) μ, tips incrassate to sharp, in 1 row. Cauda rounded; caudal protuberance moderately to poorly developed, sometimes absent; length of longest caudal setae: 48–103 (75 ± 12) μ, tips sharp. LEGS: Length of metafemora: 469–938 (718 ± 126) μ; metatibiae: 653–

1397 (1042 ± 195) μ; longest dorsal setae on central one-third of metatibiae: 8–118 (58 ± 33) μ, tips 0.1–3.0× diameter of metatibiae, tips incrassate to sharp; approximately equal or very gradually increasing distally, no setal length dimorphism, but very rarely with dorsal setae breaking on proximad one-third of metatibiae to a ca. 30–50 percent increase in length; longest ventral setae on metatibiae: 14–73 (35 ± 14) μ, tips sharp. Length of metabasitarsus: 84–148 (122 ± 16) μ; metadistitarsus: 148–230 (191 ± 20) μ. Ratio of metadistitarsus to metabasitarsus less than 1.9:1, mean 1.57:1. *Pigmentation:* Color in life: Thorax gray-green, abdomen lime green, legs light to dark brown, or straw yellow throughout; dorsal spots absent to brown. Slide-mounted specimens: Background of body dorsum pale to moderate brown (usually to 20, infrequently to 40 percent pigment density), unicolorous. Terga at bases of setae on frons and dorsal (major + minor) setae on abdomen concolorous with surrounding terga, to conspicuously darker. Thoracic muscle attachment plates and dorsal muscle attachment plates of abdomen, spiracular plates and ventral abdominal sclerites pale, inconspicuous, to dark brown, conspicuous. Siphunculi concolorous with surrounding terga, to substantially darker. Cauda, anal and subgenital plates concolorous with abdominal terga, to substantially darker. Antennal segments V and IV subtly dusky distally, pale proximally, to entirely dusky; III entirely very pale to subtly dusky on distal one-third, remainder pale; II concolorous with proximal III, to subtly darker; I concolorous with frons. Pro-, meso- and metatibiae usually concolorous, evenly pale or pale with subtly dusky distal tip, to evenly dark brown; or metatibiae subtly to substantially darker than pro- and mesotibiae. Distitarsi dusky on distal one-third, pale proximally, to evenly dark brown with tibiae.

Ultimate Stadium Nymphs of Viviparous Apterae.—Slide-mounted specimens: Nonmorphometrics as described for viviparous apterae except lacking body dorsum pigmentation suite; abdominal terga membranous with dorsal (major + minor) setae, between muscle attachment plates, arising from distinct scleroites. Mesonotum lacking 2 sclerotized plates extending from muscle attachment sites to engulf neighboring setal bases; area surrounding muscle attachment sites membranous.

Viviparous Alatae.—Slide-mounted specimens: Nonmorphometrics as described for viviparous apterae except lacking body dorsum pigmentation suite; abdominal terga normally membranous, dorsal (major + minor) setae between muscle attachment plates occasionally arising from distinct scleroites; antennal segments often as dark as tibiae, except proximal one-fifth of III pale. Antennal segment III with 0–5, IV with 0–3, secondary rhinaria. Epicranial suture strongly developed. Forewing medius with single furcation arising on proximad, very rarely on central, one-third of vein; cubital base arising proximad, rarely distad, on subcosta with distance between anal and cubital bases on subcosta usually relatively small, ca. 20–30 percent or less of anal vein length; medius, especially cubitus and anal veins usually distinct, except infrequently proximad 10–15 percent vague. Abdominal terga lacking irregular sclerites that engulf or join muscle attachment plates and dorsal (major + minor) setal bases or scleroites.

Oviparae.—Slide-mounted specimens: Nonmorphometrics as described for viviparous apterae except abdominal dorsum membranous with irregular transverse sclerites containing dorsal (major + minor) setae, occasionally dorsal muscle attachment plates, on each tergum; marginal setae usually on separate scleroites, occasionally engulfed by dorsal sclerites on posterad terga; siphuncular cones sclerotized, regular, separated from other dorsal sclerotic fields; dorsal abdominal muscle attachment plates unicolorous. Rarely with abdominal II–VI sclerotic/fused, terga VII and VIII free; dorsal demarcations of anterad terga then evident and siphuncular cones surrounded closely by, sometimes engulfed by, sclerotic fields. Pseudorhinaria on metatibiae irregular, 12–21; also on procoxa and pro- and metafemora (Essig 1909: figs. 2a–b, 2d).

Males.—Slide-mounted specimens: Nonmorphometrics as described for viviparous apterae except body slightly smaller, with slightly longer antennae and tibiae; dorsal demarcations of abdominal terga evident. Antennal segment III with 13–15, IV with 8–10, secondary rhinaria.

Fundatrices.—Slide-mounted specimens: Nonmorphometrics as described for viviparous apterae except siphunculi absent; longest dorsal setae on central part of metatibiae 0.5–1.5× tibial diameter.

Diagnosis.—*Essigella* (*E.*) *californica* requires the combination of several characters for identification; individuals usually are pale and may be confused with other pale *Essigella*. *Essigella* (*E.*) *californica* can be separated from all *Essigella,* except *E.* (*E.*) *hoerneri* and *E.* (*E.*) *pini* by having six (Fig. 1F), instead of eight or more, dorsal (major + minor) setae on abdominal terga III–IV. *Essigella* (*E.*) *californica* differs from *E.* (*E.*) *pini* by having usually small and irregular, rather

than large, ventral abdominal sclerites on abdominal segments III–IV, and also small and noninvasive, rather than large and invasive, muscle attachment plates on the mesonotum of later stadia nymphs of apterae. Alates differ from those of *E.* (*E.*) *pini* by having the forewing medius always 1-branched with the furcation proximad, near the subcosta, instead of usually unbranched or occasionally 1-branched but with the furcation no more distad than half way between the subcosta and the posterad margin of the wing, as in *E.* (*E.*) *pini*. Oviparae of *E.* (*E.*) *californica* and *E.* (*E.*) *pini* differ in the sclerotic pattern of the abdominal dorsum; in *E.* (*E.*) *pini,* usually all terga, except terga I and VIII, are fused; in *E.* (*E.*) *californica,* usually all terga are separate (as independent sclerotic bands), or infrequently segments II–VI are (sometimes only partially) united, with evident segmental demarcations, but terga VII and VIII remain independent [*E.* (*E.*) *pini* rarely shows the latter condition].

Essigella (*E.*) *californica* and *E.* (*E.*) *hoerneri* are difficult to distinguish; the qualitative characters listed above for alates, oviparae and nymphs are identical between them. Although *E.* (*E.*) *californica* has a shorter rostrum, narrower head and longer antennal segment IV than does *E.* (*E.*) *hoerneri,* these differences are indiscrete and reliable separation requires application of the discriminant function in the key to the viviparous apterae [couplets 27 or 28, see 26].

Synonyms. — *Essigella claremontiana* Hottes, NEW SYNONYM: holotype, vivip. apt., on slide with 5 other apt., holotype shown by arrow (11 o'clock position); data: CALIFORNIA. *LOS ANGELES Co.:* Claremont, 14 Feb 1909, *Pinus radiata. Essigella claremontiana* holotype deposited in the NMNH.

Essigella cocheta Hottes, NEW SYNONYM: holotype, vivip. apt., on slide with 9 other apt. (including the holotype of *E. monelli*), *E. cocheta* holotype shown by circle (7 o'clock position); data: CALIFORNIA. *MENDOCINO Co.:* Fort Bragg, 8 May 1936, E.O.E[ssig]., *Pinus "tuberculata"* [= *P. muricata*]. *Essigella cocheta* holotype is deposited in the Essig Museum of Entomology, University of California at Berkeley, Berkeley, California.

Essigella monelli Hottes, NEW SYNONYM: holotype, vivip. apt., on same slide as holotype of *E. cocheta* (see above), *E. monelli* holotype shown by circle (12 o'clock position). *Essigella monelli* holotype data and depository same as *E. cocheta,* above.

Essigella pineti Hottes, NEW SYNONYM: holotype vivip. alat., on slide with fundatrix of *E.* (*L.*) *fusca voegtlini*; data: CALIFORNIA. *MARIPOSA Co.:* Yosemite, 1218 m (4000 ft), 17 May 1938, E.O.E.[ssig]., *Pinus ponderosa. Essigella pineti* holotype is deposited in the Essig Museum of Entomology, University of California at Berkeley, Berkeley, California.

Essigella swaini Hottes, NEW SYNONYM: holotype, vivip. alat., on slide with 6 other specimens, holotype shown by circle (12 o'clock position); data: CALIFORNIA. *LAKE Co.:* Kelseyville, 12 Apr 1936, P. Schulthess, *Pinus sabiniana. Essigella swaini* holotype is deposited in the Essig Museum of Entomology, University of California at Berkeley, Berkeley, California.

Range. — Southern British Columbia and Alberta, throughout the western U.S. (exclusive of Alaska), to southern Mexico (Fig. 8); extensive sampling (Sorensen 1983) has most commonly collected it west of the Cascade-Sierra Nevada ranges and through Arizona and New Mexico. One confirmed record from Miami, Florida suggests it may occur in the Caribbean and have a Pan-Mexican distribution.
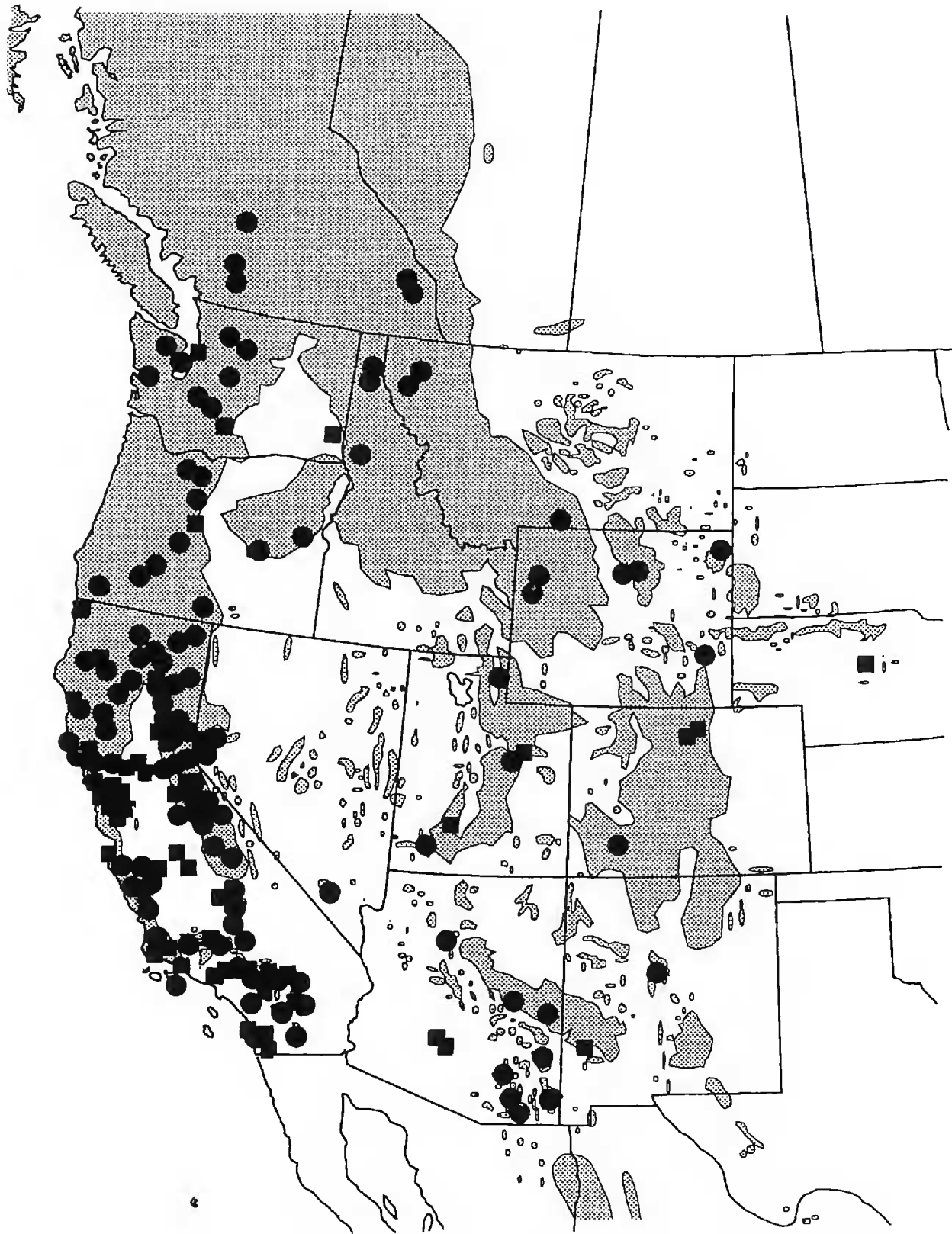
Figure 8. Distribution of *E.* (*E.*) *californica* [dots (JTS samples), squares (nonJTS samples)], superimposd over an amalgamation of the ranges of its hosts. Collections (not shown) also exist in southern Florida, central Mexico, France and Spain.

Recently (Turpeau & Remaudiere 1990), I have identified it as having been introduced into France, in *Pinus radiata* plantations; since then, it has also been found in Spain (Seco Fernandez & Mier Durante 1992).

Hosts.—*Pinus* and *Pseudotsuga*. Frequently found on: *Pinus albicaulis* Engelmann, *P. monticola, P. flexilis, P. leiophylla, P. ponderosa, P. ponderosa* var. *arizonica, P. jeffreyi, P. engelmannii, P. sabiniana, P. coulteri, P. torreyana* Parry, *P. radiata, P. attenuata, P. muricata*; infrequently found on: *Pinus strobiformis, P. lambertiana, P. contorta latifolia* Engelmann ex S. Watson, *P. washoensis* Mason & Stockwell, *Pseudotsuga menziesii* (Mirbel) Franco, *Pseudotsuga macrocarpa* (Vasey) Mayr; not found on: *Pinus cembroides* Zuccagni, *P. edulis* Engelmann, *P.*

monophylla, P. quadrifolia, P. balfouriana Greville & Balfour, *P. aristata* Engelmann, *P. contorta contorta, P. contorta murrayana, P. contorta bolanderi* (Sorensen 1983). During a recent introduction in France, Turpeau & Remaudiere (1990) report *P. rigida, P. strobus, P. taeda, P. virginiana* and *P. griffithi* McClelland as additional hosts.

Essigella (*E.*) *californica* is frequently abundant on nonnative pines in the central valley of California, and also on native pines, especially subsection Sabinianae, in the surrounding foothills and in southern California. Although it is quite polyphagous within *Pinus,* it is notably absent on pinyon pines [see discussion of *E.* (*E.*) *hoerneri*]. It occasionally feeds on *Pseudotsuga,* but apparently not in the presence of *E.* (*E.*) *wilsoni.* Although *E.* (*E.*) *californica* may occur on hosts that are occupied by other, more restricted *Essigella* species, it is generally less numerous (i.e., relative abundance on an individual tree) on such hosts than are the species that are restricted to that niche; this is especially true when both occur on an individual tree.

Note that with reference to "Sp. A" [= *E.* (*E.*) *californica*], Sorensen (1987a: 255, lines 27, 28) mentioned *Pseudotsuga* as a "(secondary host capture)"; this unfortunate wording refers to opportunistic capture of a host species as a primary host, not a secondary (i.e., summer) host in the sense of the life cycle of the aphidines.

Discussion.—This species, together with *E.* (*E.*) *hoerneri,* forms the *E.* (*E.*) *californica* complex. *Essigella* (*E.*) *californica* is the commonest *Essigella* in the western Nearctic and appears to be the species [followed closely by *E.* (*E.*) *hoerneri*] that is most prone to produce alates, as determined by their frequency among and within collection samples. This species is operationally defined and may actually represent a series of sibling entities on different host groups; however, I am comfortable with considering it to be a single taxon, because the range of its morphological variance does not appear to significantly exceed that shown by other, less polyphagous *Essigella* species. Further taxonomic division, beyond the current operational level, seems unwarranted unless biological and genetic analyses are carried out.

Essigella (*E.*) *californica* and *E.* (*E.*) *hoerneri* share several nonexclusive apomorphies, although I have no doubt that they form a monophyletic group: reduction of the dorsal (major + minor) setae to six [shared with *E.* (*E.*) *pini*] and the marginal setae to two [with *E.* (*E.*) *pini, E.* (*E.*) *wilsoni* and *E.* (*E.*) *alyeska*] on abdominal terga III–IV; reduction of the ventral abdominal sclerites on segments III–IV to small, irregular plates [with *E.* (*E.*) *wilsoni* and, in part, *E.* (*E.*) *alyeska, E.* (*L.*) *fusca, E.* (*L.*) *hillerislambersi* and (rarely) *E.* (*E.*) *pini*]; and the reduction of the mesonotal muscle attachment plates on the latter stadia apterae nymphs to noninvasive [with *E.* (*E.*) *wilsoni, E.* (*E.*) *alyeska,* and (very rarely) *E.* (*E.*) *pini*].

I have analyzed character variation among and within populations of the *E.* (*E.*) *californica* complex, in comparison to the *E.* (*L.*) *fusca* and *E.* (*E.*) *knowltoni* complexes, using principal component analyses (unpublished data). In those analyses, the body setal lengths of the former generally loaded uniformly and heavily on the second principal component vector, with the first vector representing general-size. The extent of that setal loading was generally much more uniform for the *E.* (*E.*) *californica* complex, than it was for these other complexes, indicating

that setal lengths vary more, in unison, in the *E. (E.) californica* complex than in either of the others. In other analyses (unpublished data), when only *E. (E.) californica* and *E. (E.) hoerneri* were subjected to principal component analysis, where general-size was again represented by vector 1, they diverged on combinations of vectors 2 versus 3. The loadings of those vectors indicated that their separation was chiefly on the basis of body widths and stylet length. In contrast, Hottes (1957: 109, key couplet 11) used 0.030 mm as a threshold value for the length of the dorsal setae on the metatibia (his "hairs on the mid region of outer margin of metathoracic tibiae") to separate his *E. "californica"* and *E. "hoerneri"*; clearly Hottes' approach was erroneous.

Essigella (E.) californica and *E. (E.) hoerneri* show extreme variation of the length of the setae on the frons and dorsal setae on the metatibiae. This population attribute could be considered synapomorphic, as a mutation that allows greater phenotypic plasticity of setal length in response to environmental conditions, but the mechanism of expression is not understood. *Essigella (E.) wilsoni* also shows a similar tendency, but to a lesser degree; the number of incidences of extreme setal length reduction (i.e., < 0.3× tibial diameter) is much less in it.

Other variation shared by both *E. (E.) californica* and *E. (E.) hoerneri* entails the relative length of the metatibiae on adult viviparous apterae. On occasion, aberrant individual viviparous apterae retain the relatively shorter metatibiae that is characteristic of the ultimate stadium of their nymph (i.e., the holotype of *E. "cocheta"*). This trait also occurs in other *Essigella* species, but it seems to be less frequently expressed than in the *E. (E.) californica* complex. I suspect that such aberrantly short tibiae result from the failure of a regulatory gene that controls physiognomic transitions between nymphal versus adult (or alate versus aptera) allometries.

With the exception of *E. (E.) pini*, *E. (E.) californica* has caused the greatest confusion in the genus. Hottes did not have adequate samples to reflect its variability, and used poor preparatory techniques. Among his synonyms, *E. "monelli"* and *E. "cocheta"* were stated to lack distinctly bifid tarsal claws, but their types actually have them; excessive clearing in potassium hydroxide obscures this character when viewed through only low power magnification. Other synonyms, *E. "claremontiana"* and *E. "swaini,"* were previously separated on the basis of setal lengths, which vary continuously. In fact, based upon setal length, Hottes (1957: 85) believed that the series from which Essig originally described *"Lachnus californicus"* must have had specimens of *E. "essigi"* in it [see discussion of that species]. Wilson's (1919: 1) (re)description of *"Essigella californica* (Essig)," from material on *Pseudotsuga "douglassi"* [= *P. menziesii*], *"Pinus ponderosa?"* and specimens sent to him by Essig, most probably incorporates species other than *E. (E.) californica*; if so, *E. (E.) wilsoni* and *E. (L.) fusca* might presumably be involved, but I cannot determine this.

Ironically, even Essig (1909) had some trouble recognizing the different morphs when originally describing *E. (E.) californica*. For example, Essig's illustration of an aptera of the species (Essig 1909: fig. 2a–b, 2d) clearly shows the legs with sensoria, which he mentions in the description, but the description is labeled "Apterous *Vivivarous* Female"; these are pseudorhinaria of the *ovipara* morph, however.

Coded References to This Taxon.—Essigella (E.) californica has been referred

to previously by: the coding "Sp. A" (Sorensen 1983, 1987a, 1992b) and "CALF" (Sorensen 1983), and by the name *E. californica* in Sorensen (1983).

Etymology and Common Name.—Essig named this species for California, the state in which its original collection occurred, and where it is most commonly encountered (e.g., Fig. 8). Common name: the Californian pine needle aphid; although Essig (1936: 229), Doane et al. (1936: 360), Palmer (1952: 14), and Furniss & Carolin (1977: 99) refer to this species as the "Monterey Pine Aphid," the common name indicated here is more appropriate and less confusing because *Pinus radiata,* Monterey pine, as a niche is occupied much more representatively by *E. (E.) essigi,* whereas *E. (E.) californica* is quite polyphagous within *Pinus.*

Material Examined.—ARIZONA. *COCHISE Co.:* Amer. Mus. Nat. Hist. Southwest Research Station, Chiricahua Mts, 1700 m, 16 Sep 1978, JTS 78143, *P. engelmannii,* (apt.); Carr Canyon Rd, Huachuca Mts, 2070 m, 17 Sep 1978, JTS 78155, *P. engelmannii,* (apt.); Miller Canyon Rd, Huachuca Mts, 1700 m, 17 Sep 1978, JTS 78152, *P. leiophylla,* (apt.); nr Steward Camp, Chiricahua Mts, 1530 m, 16 Sep 1978, JTS 78142, *P. leiophylla,* (apt., alat.). *COCONINO Co.:* 9 km W of Williams on hwy 66, 2070 m, 9 Sep 1978, JTS 7815, *P. ponderosa,* (apt.). *GILA Co.:* 16 km E of Kohles Ranch on hwy 260, 1700 m, 9 Sep 1978, JTS 78111, *P. ponderosa,* (apt.). *GRAHAM Co.:* SW of Stafford on hwy 366, 1830 m, 15 Sep 1978, JTS 78136, *P. leiophylla,* (apt.); same but 1980 m, JTS 78137, *P. ponderosa* var. *arizonica,* (apt.). *MARICOPA Co.:* Phoenix, 13 Jan 1972, D. Carver, *P. canariensis,* (apt.); Sun City, 27 Jan 1972, D. Carver, *P. taeda,* (apt.). *NAVAJO Co.:* Mogollon Rim Rd, 8 km SW of Showlow, 2070 m, 10 Sep 1978, JTS 78113, *P. ponderosa,* (apt.). *PIMA Co.:* Bear Canyon Picnic Area, Santa Catalina Mts, 1830 m, 18 Sep 1978, JTS 78157, *P. leiophylla,* (apt., alat.); same but JTS 78160, *P. ponderosa* var. *arizonica,* (apt.). *COUNTY UNCERTAIN:* Sitgreaves Natl Forest, 19 Jun 1969, D. T. Jennings, *P. ponderosa,* (apt.). CALIFORNIA. *ALAMEDA Co.:* Berkeley, 23 Apr 1947, E. O. Essig, *P. radiata,* (apt., alat.); same but 10 Nov 1935, (apt.); same but 28 Oct 1952, trap pan, (alat.). *ALPINE Co.:* E. side of Ebbett's Pass on hwy 4, 3 km E of summit, 2440 m, 17 Jul 1977, JTS 77G41, *P. monticola,* (apt.); same but W side, 5 km W of summit, 2500 m, JTS 77G43, *P. jeffreyi,* (apt.). *AMADOR Co.:* 13 km N of Plymouth, 29 May 1977, J. T. Sorensen, *P. sabiniana,* (apt., alat.). *BUTTE Co.:* Chico, 27 Oct 1949, H. T. Osborn, CDFA 40-K-5, *P. yunnanensis* Franchet [?], (apt., alat.); Feather River Cyn, 22 km NE of jct of hwy 70 & Cherokee Rd, 26 Jun 1977, JTS 77F14, *P. ponderosa,* (apt.). *CALAVERAS Co.:* 18 km E of Arnold on hwy 4, 1680 m, 17 Jul 1977, JTS 77G46, *P. ponderosa,* (apt.); 2 km NE of Murphys on hwy 4, 670 m, 17 Jul 1977, JTS 77G47, *P. ponderosa,* (apt.); 7 km NE of Angel's Camp on hwy 4, 460 m, 17 Jul 1977, JTS 77G48, *P. sabiniana,* (apt., alat.). *COLUSA Co.:* W of William on hwy 20, 18 Apr 1979, T. Kono & P. Crane, CDFA 79D19-35, *P. sabiniana,* (apt.). *CONTRA COSTA Co.:* Mt Diablo, 23 Apr 1939, E. O. Essig, *P. sabiniana,* (alat.); Orinda, 29 Sep 1961, E. I. Schlinger, EIS 61-9-30b, *Pinus* sp., (apt., alat.). *DEL NORTE Co.:* Gasquet, 21 Sep 1966, P. Allen, CDFA 66-116-14, *Pseudotsuga menziesii,* (alat.). *EL DORADO Co.:* Blodgett Experimental Forest (Univ. Calif.), E of Georgetown, 26 Jul 1973, D. J. Voegtlin, DJV 55, *P. ponderosa,* (apt., alat.); same but 28/29 May 1977, J. T. Sorensen, *P. lambertiana, P. ponderosa,* (alat.); Georgetown, 29 May 1977, J. T. Sorensen, *P. sabiniana,* (apt., alat.); Lake Tahoe, Meek's Bay, 1980 m, 16 Jul 1977, JTS 77G29, *P. jeffreyi,* (apt.); Mutton Cyn, 3 Oct 1961, T. Kono, *Pinus* sp., (alat.); S Fork of American River, 5 Jul 1973, D. J. Voegtlin, DJV 35, *P. sabiniana,* (apt.). *FRESNO Co.:* 22.4 km (14 mi) W of Coalinga on hwy 145, 25 Apr 1979, D. Taylor, CDFA 79D27-8, *P. sabiniana,* (apt., alat.); Clovis, 7 Apr 1965, Dunnegan, CDFA 65D9-21, *P. canariensis,* (apt.); Trimmer, Pine Flat Lake, 13 Aug 1977, JTS 77H8, *P. sabiniana,* (apt.); jct of hwys 180 & 245, 1620 m, 13 Aug 1977, JTS 77H9, *P. ponderosa,* (apt.). *HUMBOLT Co.:* nr Little River State Beach, 17 km N of Arcata on hwy 101, 4 Jul 1978, JTS 78G3, *P. muricata,* (apt., alat.). *KERN Co.:* Caliente-Bodfish Rd, S of Bodfish, 820 m, 20 Sep 1977, JTS 77I67, *P. sabiniana,* (apt.); Heritage Park, 19 Jun 1967, K. Hench, *P. canariensis* C. Smith, (apt.); Keene, 760 m, 20 Sep 1977, JTS 77I62, *P. sabiniana,* (apt.); Kernville, 22 May 1978, C. F. & C. S. Smith, CFS 78-76, *Pinus* sp., (apt., alat.); Lebec, 25 Mar 1958, E. I. Schlinger, EIS 58-3-259, *P. sabiniana,* (apt.); Tehachapi Mtn Park, S of Tehachapi, 1980 m, 19 Sep 1977, JTS 77I60, *P. ponderosa,* (apt.); same but JTS 77I61, *P. jeffreyi,* (apt.); Tiger Flat Rd, N of hwy 155, nr Alta Sierra, 1890 m, 20 Sep 1977, JTS 77I64, *P. lambertiana,* (ovip.); same but JTS 77I66, *P. jeffreyi,* (apt.). *LAKE Co.:* 10 km S of Lake Pillsbury, Elk Mt Rd, 930 m, 24 Jul 1977, JTS 77G57,

P. ponderosa, (apt., alat.); same but 5 km S, 640 m, JTS 77G56, *P. jeffreyi,* (apt.); 21 km N of Upper Lake, Elk Mt Rd, 1030 m, 24 Jul 1977, JTS 77G60, *P. attenuata,* (alat.); Kelseyville, 12 Apr 1936, P. Schulthess, *P. sabiniana,* (apt.); same but 15 Jul 1935, E. Doybell, (alat.); W of Lake Pillsbury, Eel River Rd, 340 m, 24 Jul 1977, JTS 77G54, *P. sabiniana,* (apt., alat.). *LASSEN Co.:* 7 km SW of Susanville on hwy 36, 1460 m, 4 Jul 1977, JTS 77G13, *P. jeffreyi,* (apt., alat.); Lassen Natl Park, summit area, 2440 m, 10 Jul 1977, JTS 77G18, *P. monticola,* (apt.); hwy 89 (nr Lassen Natl Park), 6 km N of jct with hwy 36, 2013 m, 10 Jul 1977, JTS 77G20, *P. monticola,*(apt.). *LOS ANGELES Co.:* (lectotype) Claremont, 14/18 Feb 1909, E. O. Essig, *P. radiata,* (apt., alat.); Lake Hughes, 22 May 1959, E. I. Schlinger, EIS 59-5-23k, *P. ponderosa,* (alat.); same but 2 km NE on hwy N2, 1000 m, 18 Sep 1977, JTS 77I52, *P. sabiniana,* (apt.); 3 km SE of Big Pines on hwy 2, E of Blue Ridge Summit, 2200 m, 17 Sep 1977, JTS 77I49, *P. jeffreyi,* (alat.); Azuza, 4 Nov 1969, McHorn & Weber, CDFA 69K7-8, *P. canariensis,* (apt.); Camp Baldy, 5 Dec 1956, J. MacSwain, "on fir," (apt., alat.); hwy 2, 7 km NE of jct with Mt Wilson Rd, San Gabriel Mts, 1530 m, 18 Sep 1977, JTS 77I51, *P. coulteri,* (apt.). *MARIN Co.:* San Rafael, 18 May 1967, C. Schmid, *P. radiata,* (apt.). *MARIPOSA Co.:* Feliciana Mt, 25 Jul 1946, H. Chandler, *P. "tuberculata"* [= *muricata*?], (apt.); Yosemite Natl Park, Camp Foresta, 1340 m, 30 Jul 1977, JTS 77G64, *P. ponderosa,* (apt., alat.); same but JTS 77G65, *P. lambertiana,* (apt.). *MENDOCINO Co.:* 10 km W of Laytonville, Branscomb Rd, 580 m, 24 Jul 1977, JTS 77G53, *P. ponderosa,* (apt.); Albion-Little River Rd, 5 km E of hwy 1, 210 m, 23 Jul 1977, JTS 77G52, *P. muricata,* (apt., alat.); Fish Rock Rd, 7 km E of Anchor Bay, 23 Jul 1977, JTS 77G51, *P. muricata,* (apt.); Fort Bragg, 8 May 1936, E. O. Essig, *P. "tuberculata"* [= *muricata*?], (apt.). *MODOC Co.:* 1 km W of Adin Pass on hwy 299, 21 Jul 1978, JTS 78G120, *P. ponderosa,* (apt.); E side of Cedar Pass, 29 km E of Alturas, 1890 m, 3 Jul 1977, JTS 77G12, *P. ponderosa,* (apt.). *MONO Co.:* Deadman Summit on hwy 395, nr Crestview, 2440 m, 31 Jul 1977, JTS 77G72, *P. jeffreyi,* (apt.); Saddlebag Lake, 3050 m, 31 Jul 1977, JTS 77G69, *P. albicaulis,* (apt., fund.). *MONTEREY Co.:* Cone Mt, 9 Aug 1962, E. I. Schlinger, EIS 62-8-9a, *Pinus* sp., (apt.); Cone Peak Rd, 2 km N of jct with Nacimento-Fergusson Rd, Los Padres Natl Forest, 910 m, 4 Sep 1977, JTS 77I9, *P. coulteri,* (apt.); Lockwood-San Ardo Rd, 13 km SW of jct with Paris Valley Rd, 550 m, 4 Sep 1977, JTS 77I7, *P. attenuata,* (apt.); same but JTS 77I8, *P. sabiniana,* (apt.); Monterey, 16 Feb 1979, T. Kono, CDFA 79B20-10-3, *P. radiata,* (apt.); same but 18 Jun 1973, D. J. Voegtlin, DJV 24, *P. radiata,* (apt., alat.). *NAPA Co.:* 16 km NE of Angwin, jct of Howell Mt Rd & Pope Canyon Rd, 4 Feb 1978, JTS 79B1, *P. sabiniana,* (apt.). *ORANGE Co.:* Anaheim, 9 Feb 1965, J. Seapy, CDFA 65B15-26-2, *P. radiata,* (apt.); above Santiago Peak Rd, 10 km N of jct with hwy 74, Cleveland Natl Forest, 1220 m, 10 Sep 1977, JTS 77I22, *P. coulteri,* (apt.); same but JTS 77I23, *P. attenuata,* (apt.). *PLACER Co.:* 5 km SW of Whitmore on hwy 80, 1430 m, 25 Jun 1977, JTS 77F1, *P. ponderosa,* (apt.); 6 km W of Dutch Flat on hwy 80, 2 Aug 1978, JTS 78H2, *P. attenuata,* (apt.); same but 27 Aug 1978, JTS 78H160, (apt.). *PLUMAS Co.:* 13 km E of Chester on hwy 36, 1520 m, 4 Jul 1977, JTS 77G15, *P. jeffreyi,* (apt., alat.); hwy 36, 6 k W of jct with hwy 89, 1460 m, 10 Jul 1977, JTS 77G22, *P. lambertiana,* (apt.); same but JTS 77G25, *P. jeffreyi,* (apt.); Jackson Creek Cmpgd, Plumas Natl Forest, 2 km SE of Cromberg on hwy 70/89, 1280 m, 26 Jun 1977, JTS 77F12, *P. ponderosa,* (apt.); Keddie, 18 Oct 1966, Swanson, CDFA 66J24-27, *Pseudotsuga menziesii,* (apt.). *RIVERSIDE Co.:* Idyllwild, 1 Jun 1940, C. Michner, *P. ponderosa,* (apt., alat.); Keen Camp Summit on hwy 74, 3 km N of Mountain Center, San Bernardino Natl Forest, 1500 m, 9 Sep 1977, JTS 77I20, *P. coulteri,* (apt.); Riverside, 28 Nov 1961, C. Lagace, EIS 61-2-28a, *P. canariensis,* (apt., alat.); same but 9 Mar 1960, E. I. Schlinger, EIS 60-3-9a, *P. canariensis,* (apt., alat.). *SACRAMENTO Co.:* Wm. Land Park, Sacramento, 26 Aug 1961, T. Kono, *Pinus* sp., (apt., alat.). *SAN BENITO Co.:* Clear Creek Rd, 10 km SE of jct with Coalinga Rd, 1000 m, 3 Sep 1977, JTS 77I4, *P. coulteri,* (apt.); same but 14 km SE of that jct, 1370 m, JTS 77I5, (apt., alat.); same but Clear Creek Recreation Area entrance, 2600 m, JTS 77I6, *P. sabiniana,* (apt.); Coalinga Rd, 2 km SE of jct with hwy 25, 550 m, 3 Sep 1977, JTS 77I3, *P. sabiniana,* (apt.); Gloria-Bickmore Rd, 14 km W of jct with hwy 25, 580 m, 3 Sep 1977, JTS 77I1, *P. sabiniana,* (apt.); same but JTS 77I2, *P. coulteri,* (apt.); Pinnacles Natl Monument, 24 Apr 1948, J. MacSwain, *Pinus* sp., (apt.). *SAN BERNARDINO Co.:* 7 km W of Barton Flat on hwy 38, 1950 m, 16 Sep 1977, JTS 77I36, *P. coulteri,* (apt., alat.); San Bernardino Natl Forest, Keller Peak Cmpgd, 2200 m, 17 Sep 1977, JTS 77I42, *P. attenuata,* (apt.); same but Dogwood, 28 Aug 1972, D. J. Voegtlin, DJV 72, *P. ponderosa,* (alat.); same but Running Springs, 4 Aug 1973, DJV 77, *P. coulteri,* (alat.); same but Snow Valley, 28 Aug 1972, DJV 69, *P. jeffreyi,* (alat.); Redlands, 22 Dec 1978, CDFA 78L26-28, *P. radiata,* (apt.). *SAN DIEGO Co.:* 2 km E of Mt Palomar on hwy S6, 1650 m, 11 Sep 1977, JTS 77I28, *P. attenuata,* (apt.); Mt Palomar Rd (hwy S6), 5 km S of Mt Palomar, 1370 m, 11 Sep 1977, JTS 77I26, *Pseudotsuga macrocarpa,* (apt.); 5 km S of Julian, Harrison Springs Rd, 1460 m, 12 Sep 1977, JTS

77129, *P. coulteri,* (apt.); La Jolla, Univ. Calif. campus, 11 Sep 1977, JTS 77125, *P. torreyana,* (apt., alat.); San Diego, 10 May 1967, R. Roberson, CDFA 67E15-68, *P. radiata,* (apt.); same but 29 Jun 1961, O. Beck, CDFA 61F29-53, (apt., alat.); same but 11 Dec 1957, W. Radcliffe, *P. canariensis,* (apt., alat.); Torrey Pines State Reserve, 10 Sep 1977, JTS 77124, *P. torreyana,* (apt.); Valley Center, 18 Apr 1975, G. Gordun, CDFA 75D24-34, *Pinus* sp., (apt.). *SAN FRANCISCO Co.:* San Francisco, 28 Apr 1967, M. Stufflebeam, CDFA 67E1-10, *P. radiata,* (apt., alat.). *SAN LUIS OBISPO Co.:* 2 km E of Santa Margarita on hwy 58, 300 m, 5 Sep 1977, JTS 77113, *P. sabiniana,* (apt.); Cuesta Ridge Botanical Area, nr La Cuesta Summit on hwy 101, N of San Luis Obispo, 730 m, 5 Sep 1977, JTS 77114, *P. coulteri,* (apt., alat.); Ragged Point, 21 Jul 1973, D. J. Voegtlin, DJV 56, *P. radiata,* (alat.). *SANTA BARBARA Co.:* Happy Canyon Rd, 16 km NE of jct with hwy 154, Los Padres Natl Forest, 370 m, 6 Sept 1977, JTS 77116, *P. sabiniana,* (apt., alat.); Purissima Hills, 10 km N of jct of hwys 1 & 246, 6 Sept 1977, JTS 77115, *P. muricata,* (apt., alat.); San Marcos Pass, 740 m, 14 Apr 1960, E. I. Schlinger & J. Hall, EIS 60-4-15c, *P. "monticola"* [?], (apt., alat.); Santa Barbara, 1 May 1939, G. Woodham, *Pinus* sp., (apt., alat.); Santa Cruz Island, Prisoner's Harbor, 25 Sep 1978, JTS 78164, *P. muricata,* (apt.); Santa Ynez, 23 Apr 1975, B. Jarvis, CDFA 75D24-39, *Pinus* sp., (apt.); Tequepis Cyn, 17 May 1957, M. Cravens, CDFA 57E21-14, *P. radiata,* (apt.). *SANTA CLARA Co.:* Campbell, 19 Apr 1967, G. Prole, CDFA 67E5-34, *Pinus* sp., (apt.); Palo Alto, Stanford Univ., 25 Apr 1930, P.S.B., *P. radiata,* (apt.); same but 7 Apr 1912, H. Morrison, *P. "maritima"* [?], (apt., alat.). *SANTA CRUZ Co.:* Santa Cruz, 20 Jul 1966, J. Bauer, CDFA 66G26-3, *Pinus* sp., (alat.). *SHASTA Co.:* 24 km (15 mi) E of Redding, nr Bella Vista, 29 Mar 1979, D. Henry, CDFA 79C29-19, *P. sabiniana,* (apt.); 16 km S of Castella on hwy 5, 400 m, 2 Jul 1977, JTS 77G1, *P. sabiniana,* (apt.); 2 km W of Fall River Mills on hwy 299, 21 Jul 1978, JTS 78G121, *P. sabiniana,* (apt., alat.); same but JTS 78G123, *P. ponderosa,* (apt.); 3 km N of hwy 299 on Rock Creek Rd, W of Redding, 300 m, 20 Aug 1977, JTS 77H14, *P. attenuata,* (apt.); Whiskeytown Lake, 370 m, 20 Aug 1977, JTS 77H15, *P. attenuata,* (apt.); same but JTS 77H16, *P. sabiniana,* (apt., alat.). *SISKIYOU Co.:* Edson Creek access Rd, Shasta Natl Forest, 8 km W of Bartel on hwy 89, 1160 m, 3 Jul 1977, JTS 77G10, *P. jeffreyi,* (apt., alat.); Mt Shasta Ski Bowl Rd, 2450 m, 2 Jul 1977, J. T. Sorensen & D. J. Voegtlin, JTS 77G8, *P. lambertiana,* (apt.); same but JTS 77G6, *P. ponderosa,* (apt., alat.); same but JTS 77G4, *P. albicaulis,* (apt., fund.); Snowman Hill Summit on hwy 89, 8 km E of jct with hwy 5, 1360 m, 2 Jul 1977, JTS 77G2, *P. ponderosa,* (apt., alat.). *SOLANO Co.:* Green Valley, 29 Oct 1939, N of Frazier, (alat.). *SONOMA Co.:* hwy 101, at Sonoma-Mendocino Co. line, 3 Jul 1978, JTS 78G1, *P. sabiniana,* (apt., alat.). *TEHAMA Co.:* 29 km E of Dales on hwy 36, 910 m, 10 Jul 1977, JTS 77G27, *P. sabiniana,* (apt., alat.); same but 970 m, JTS 77G28, *P. ponderosa,* (apt., alat.); Lanes Valley Rd, nr jct with hwy 36, 490 m, 4 Jul 1977, JTS 77G17, *P. sabiniana,* (apt.). *TRINITY Co.:* Big Flat, 1 Jun 1978, C. F. Smith, *P. sabiniana,* (apt.); Buckhorn Summit on hwy 299, W of Tower House, 980 m, 20 Aug 1977, JTS 77H17, *P. ponderosa,* (apt., alat.); Weaverville, 550 m, 20 Aug 1977, JTS 77H20, *P. sabiniana,* (apt., alat.); same but JTS 77H21, *P. ponderosa,* (apt., alat.). *TULARE Co.:* E of Big Meadows Cmpgd, Sierra Natl Forest, 2320 m, 13 Aug 1977, JTS 77H13, *P. jeffreyi,* (apt.); same but JTS 77H12, *P. monticola,* (apt.); Visalia, 9 Apr 1971, J. Gilley, CDFA 71D12-11, *Pinus* sp., (apt., alat.). *TUOLUMNE Co.:* 2 km E of Groveville on hwy 120, 910 m, 30 Jul 1977, JTS 77G63, *P. ponderosa,* (apt., alat.); 7 km W of Big Oak Flat on hwy 120, 550 m, 30 Jul 1977, JTS 77G61, *P. sabiniana,* (apt.); Kennedy Meadows, 12 Jul 1951, W. Lange, *P. ponderosa,* (alat.); Mocassin, 14 Jun 1973, D. J. Voegtlin, DJV 37, *P. sabiniana,* (apt., alat.); Strawberry, 26 Apr 1951, J. MacSwain, *Pinus* sp., (alat.); Yosemite Natl Park, 1330 m, 17 May 1938, E. O. Essig, *P. ponderosa,* (alat.). *VENTURA Co.:* 4.8 km (3 mi) S of Pine Mt Summit, 16 May 1961, R. Van den Bosch, RVdB 61-V-19j, *P. sabiniana,* (apt., alat.); Mt Pinos Summit, 2684 m, 18 Sep 1977, JTS 77154, *P. flexilis,* (apt., ovip., male); Santa Paula, 26 Jun 1911, E. O. Essig (USNM type 16243, *P. radiata,* (apt., alat.). *YOLO Co.:* Davis, 1 Mar 1979, R. Harris, CDFA 79C2-1-2, *P. sabiniana,* (apt., alat.); Davis, 19 May 1979, T. & C. Kono, CDFA 79E21-42, *P. sabiniana,* (apt.). COLORADO. *LARIMER Co.:* Stove Prairie Hill, nr Bellvue, 16 Jun 1922, M. A. Palmer, CAES 3118, *P. "murraryana"* [= *contorta latifolia*?], (alat.); Estes Park, 22 Jul 1922, M. A. Palmer, CAES 3152, *P. flexilis,* (apt.). *SAN JUAN Co.:* 20 km N of Purgatory, 3020 m, 8 Aug 1978, JTS 78H47, *P. flexilis,* (apt.). FLORIDA. *DADE Co.:* Opa Locka, 29 Feb 1956, C. Shepard & L. Daigle, *Pinus* sp., (apt.). IDAHO. *BONNER Co.:* 6 km E of Colburn on hwy 95, 18 Jul 1978, JTS 78G102, *P. monticola,* (apt.); 6 km S of Cocolalla on hwy 95, 18 Jul 1978, JTS 78G105, *P. ponderosa,* (apt., alat.). *CLEARWATER Co.:* 5 km E of Orofino on hwy 12, 18 Jul 1978, JTS 78G108, *P. ponderosa,* (apt.). MONTANA. *CARBON Co.:* E side of Beartooth pass on hwy 212, 2780 m, 20 Aug 1978, JTS 78H118, *P. albicaulis,* (apt., ovip.). *FLATHEAD Co.:* 5 km W of MacGregor Lake on hwy 2, E of Happy Inn, 18 Jul 1978, JTS 78G101, *P. ponderosa,* (apt., alat.); hwy 93, nr Olney, 17 Jul 1978, JTS

78G99, *P. monticola,* (apt.). NEBRASKA. *THOMAS Co.:* Halsey, 14 Sep 1958, R. Henzlik, (alat.). NEVADA. *CLARK Co.:* Charleston Mts, Lee Canyon Ski Area, 2590 m, 4 Aug 1978, JTS 78H16, *P. flexilis,* (apt., alat.). *WASHOE Co.:* Mt Rose Summit Cmpgd, Toiyabe Natl Forest, 2 Aug 1978, JTS 78H8, *P. albicaulis,* (apt., fund.); same but JTS 78H9, *P. monticola,* (apt.); Mt Rose, Slide Mountain Ski Area, 2 Aug 1978, JTS 78H6, *P. washoensis,* (apt.). NEW MEXICO. *BERNALILLO Co.:* 2 km NW of San Antinito on hwy 44, 2290 m, 12 Sep 1978, JTS 78I20, *P. ponderosa,* (apt.). *CATRON Co.:* Apache Natl Forest, 11 May 1978, C. F. & C. S. Smith, CFS 78-24, (apt., alat.). OREGON. *BAKER Co.:* 11 km W of Unity on hwy 26, 20 Jul 1978, JTS 78G112, *P. ponderosa,* (apt., alat.). *CLACKAMAS Co.:* Timberline Lodge, Mt Hood, 1770 m, 6 Jul 1978, JTS 78G35, *P. albicaulis,* (fund.). *DESCHUTES Co.:* Sisters, 23 May 1968, C. F. Smith & B. Zak, CFS 68-115, *P. ponderosa,* (apt.). *HARNEY Co.:* 20 km N of Burns on hwy 395, 20 Jul 1978, JTS 78G117, *P. ponderosa,* (apt., alat.). *JACKSON Co.:* 21 km S of Union Creek on hwy 62, 5 Jul 1978, JTS 78G15, *P. ponderosa,* (apt., alat.); same but 3 km E, 110 m, JTS 78G18, (apt). *JOSEPHINE Co.:* O'brien, 4 Jul 1978, JTS 78G9, *P. jeffreyi,* (apt.). *KLAMATH Co.:* 16 km S of LaPine on hwy 97, 5 Jul 1978, JTS 78G26, *P. ponderosa,* (apt., alat.). *LAKE Co.:* 28 km N of Lakeview on hwy 395, 20 Jul 1978, JTS 78G119, *P. ponderosa,* (apt.). *WASCO Co.:* 21 km SE of Government Camp on hwy 26, 970 m, 6 Jul 1978, JTS 78G34, *P. monticola,* (apt.); same but 46 km SE, 670 m, JTS 78G32, *P. c. murrayana,* (apt., alat.); jct of Mills Creek & hwy 26, 35 km NW of Madras, 6 Jul 1978, JTS 78G29, *P. ponderosa,* (apt., alat.). UTAH. *CACHE Co.:* Bearlake Summit on hwy 89, 8 km W of Garden City, 2350 m, 24 Aug 1978, JTS 78H132, *P. flexilis,* (apt.). *DUCHESNE Co.:* 19 km NE of Castle Gate on hwy 33, 2770 m, 25 Aug 1978, JTS 78H144, *P. flexilis,* (apt.); W of Duchesne, 29 Jun 1958, G. F. Knowlton, (alat.). *IRON Co.:* 32 km SE of Cedar City on hwy 14, 3020 m, 5 Aug 1978, JTS 78H27, *P. flexilis,* (apt.). *PIUTE Co.:* Marysville Cyn, 11 Jun 1943, G. F. Knowlton, *P. ponderosa,* (alat.). WASHINGTON. *CHELAN Co.:* 8 km SW of Chelan on hwy 97, 12 Jul 1978, JTS 78G68, *P. ponderosa,* (apt., alat.); Washington Pass on hwy 20, 1700 m, 12 Jul 1978, JTS 78G75, *P. albicaulis,* (apt., fund.). *CLALLAM Co.:* Olympic Natl Park, Hurricane Ridge, 9 Jul 1978, JTS 78G51, *P. monticola,* (apt., fund.). *GRAYS HARBOR Co.:* 16 km W of Amanda Park on hwy 101, 10 Jul 1978, JTS 78G54, *P. monticola,* (apt.). *KING Co.:* Seattle, 16 Jun/20 Oct 1955, M. Forsell, *Pinus* sp., (apt.). *KITSAP Co.:* 8 km S of Hood Canal bridge on hwy 3, 9 Jul 1978, JTS 78G49, *P. monticola,* (apt.). *OKANOGAN Co.:* 17 km NW of Winthrop on hwy 20, 550 m, 12 Jul 1978, JTS 78G71, *P. ponderosa,* (apt., alat.). *WHITMAN Co.:* Pullman, 26 Sep 1956, F. C. Hottes, *P. ponderosa,* (alat.). *YAKIMA Co.:* 16 km W of Naches on hwy 410, 11 Jul 1978, JTS 78G65, *P. ponderosa,* (apt.); E side of Chinook Pass on hwy 410, 1310 m, 11 Jul 1978, JTS 78G63, *P. monticola,* (apt.); Union Gap, 22/26 Sep 1952, E. Davies, trap pan, (alat.). WYOMING. *CROOK Co.:* 6 km W of Devil's Tower Jct on hwy 14, 1100 m, 19 Aug 1978, JTS 78H104, *P. ponderosa,* (apt.). *PLATTE Co.:* S of Glendo on hwy 25, 1920 m, 17 Aug 1978, JTS 78H94, *P. ponderosa,* (apt.). *TETON Co.:* Hoback Jct, 19 km S of Jackson on hwy 89, 1860 m, 23 Aug 1978, JTS 78H128, *P. flexilis,* (apt., male); nr Togwotee Pass on hwy 287, 2800 m, 23 Aug 1978, JTS 78H125, *P. albicaulis,* (apt., fund., ovip.). *WASHAKIE Co.:* 19 km NE of Tensleep on hwy 16, 2350 m, 19 Aug 1978, JTS 78H107, *P. flexilis,* (apt.); Tensleep Cyn, Bighorn Mts, 1580 m, 20 Aug 1978, JTS 78H111, *P. ponderosa,* (apt.). CANADA. *BRITISH COLUMBIA:* 21 km N of Cache Creek on hwy 97, 13 Jul 1978, JTS 78G81, *P. ponderosa,* (apt.); 21 km S of Lytton on hwy 1, 13 Jul 1978, JTS 78G78, *P. ponderosa,* (apt.); 5 km N of Spuzzum on hwy 1, 13 Jul 1978, JTS 78G77, *P. monticola,* (apt., male); 7 km S of Canal Flats on hwy 93, 17 Jul 1978, JTS 78G95, *P. c. latifolia,* (apt.); Fairmont Hotsprings, hwy 93, 17 Jul 1978, JTS 78G91, *P. ponderosa,* (apt.). MEXICO. *DISTRITO FEDERAL:* Ajusco, 2800 m, 2 Apr 1981, G. Remaudiere, *Pinus* sp., (apt., alat.). *STATE UNCERTAIN:* Chapingo, 27 Oct 1980, G. Remaudiere, *Pinus* sp., (apt., alat.). FRANCE. *PROVINCE UNCERTAIN:* Rennesle Rheu, 30 Jun 1989, "R 42," piege, (alat.); Landerneau Finistere, 6 Sep 1989, E. Turpeau, 16580, "*P. radiata?,*" (apt.).

Essigella (*Essigella*) *hoerneri* Gillette & Palmer, 1924

Essigella hoerneri Gillette & Palmer, 1924: 5, Ann. Entomol. Soc. Am., 17: 5–6.
Essigella gillettei Hottes, 1957: 88, Proc. Biol. Soc. Wash., 70: 88–90. NEW SYNONYM.
Essigella maculata Hottes, 1957: 93, Proc. Biol. Soc. Wash., 70: 93–95. NEW SYNONYM.

Primary Type. —Lectotype, vivip. apt., on slide with 6 other specimens, lectotype in upper right; slide data: "*Essigella hoerneri* n. sp., lectotype (vivip. apt.) (type—others paratypes) C. P. Gillette & M. A. Palmer/U.S. Nat. Mus. No. 41952/ On *Pinus edulis,* 9-25-21, Owl Canon [sic] Larimer Co., Colo., Coll. J. L. Hoerner, Colo. Agr. Exp. Sta. Ac. 2894/[on back] lectotype, *Essigella hoerneri* Gillette & Palmer, J. T. Sorensen 1981." Lectotype deposited in the U.S. National Museum of Natural History, Washington, D.C.

There is confusion concerning the lectotype designation. In the original description, Gillette & Palmer (1924: 5–6) list no primary type, but later (Gillette & Palmer 1931: 841) state "Types in U.S. Nat. Mus., Cat. No. 41952; Paratypes in collection of Colo. Agr. Exp. Sta." Palmer (1952: 16) again refers to that museum number under the heading Type. There is a second "type" slide, containing one ovipara with four other specimens, that also bears the U.S. Nat. Mus. number 41952. Consequently, the slide cannot be identified from that number alone. Hottes (1957: 92) mentions a lectotype and gives the slide data (as above), but does not tell the position of the designated individual on the slide. Although there is a "map" of position of the "type" on the slide, I am uncertain that this represents the lectotype mentioned by Hottes. Because the "type" individual on that slide was incomplete, I have designated a different, intact specimen from the slide (upper right corner, 2 o'clock position) as lectotype.

Viviparous Apterae. —*Morphology:* Body length: 1.49–2.36 (1.86 ± 0.22) mm. HEAD: Primary rhinarium on terminal antennal segment (V) not exceptionally distad, distance from tip of processus terminalis to distal face of rhinarial rim greater than 0.5 × diameter of rhinarium; distal face of rhinarial rim usually oblique to longitudinal axis of antennal segment; rhinarial membrane not conspicuously protuberant. Length of antennal segment V: 110–148 (130 ± 10) μ, processus terminalis: 30–43 (37 ± 4) μ; IV: 75–120 (101 ± 12) μ; III: 118–238 (175 ± 29) μ; II: 59–88 (70 ± 7) μ. Length of longest setae on frons: 13–88 (48 ± 24) μ, tips incrassate to sharp. Head width: 245–329 (291 ± 22) μ. Length of stylets: 714–1130 (860 ± 107) μ; ultimate rostral segment: 58–100 (80 ± 9) μ, rostral tip reaching abdominal terga III–V in dorsal view through slide-mounted specimens. Head + pronotum fused, total length: 316–459 (385 ± 37) μ. THORAX: Meso + metanota fused, total length: 275–439 (371 ± 46) μ. ABDOMEN: Tergum I free, length: 102–148 (123 ± 13) μ; terga II–VII fused, VIII free. Maximum distal width of flange on siphunculi: 28–45 (35 ± 5) μ; siphunculi flush to truncated conical, protrusion to 0.7× maximal distal width. Ventral abdominal sclerites on segments III–IV usually irregular, subcircular or sublinear when small (length less than 0.6 × metatibial diameter), subquadrate when large (length greater than 1.0 × metatibial diameter); length: 5–51 (22 ± 11) μ, 0.3–1.1 × diameter of metatibiae. Dorsal (major + minor) setae (see Fig. 1F) on abdominal terga III–IV: 6, very rarely 7, tips sharp, in 1 row; marginal setae 2 per segment, each side. Setae on abdominal tergum VIII: 6, rarely 7, length: 13–60 (31 ± 15) μ, tips incrassate to sharp, in 1 row. Cauda rounded; caudal protuberance moderately to poorly developed, occasionally absent; length of longest caudal setae: 43–105 (78 ± 17) μ, tips sharp. LEGS: Length of metafemora: 388–857 (596 ± 106) μ; metatibiae: 561–1275 (908 ± 179) μ; longest dorsal setae on central one-third of metatibiae: 10–113 (38 ± 26) μ, 0.1–2.9 × diameter of metatibiae, tips incrassate to sharp; approximately equal or very gradually increasing distally, no setal length dimorphism; longest ventral setae on metatibiae: 18–50 (34 ± 10) μ, tips sharp. Length of metabasitarsus: 93–148 (118 ± 15) μ; metadistitarsus: 148–223 (187 ± 18) μ. Ratio of metadistitarsus to metabasitarsus less than 1.9:1, mean 1.58:1. *Pigmentation:* Color in life: Thorax gray-green, abdomen lime green, legs yellow-brown. Slide-mounted specimens: Background of body dorsum usually pale to rarely light brown (to 20 percent pigment density), usually unicolorous, occasionally abdominal terga dorsomedially dusky to entire abdomen evenly moderate brown (to 50 percent pigment density) in contrast to pale head and thorax. Terga at bases of setae on frons and dorsal (major + minor) setae on abdomen concolorous with surrounding terga, to rarely subtly darker. Thoracic muscle attachment plates and dorsal muscle attachment plates of abdomen usually pale, inconspicuous, to rarely light brown, vaguely evident. Spiracular plates and ventral abdominal sclerites pale, inconspicuous, to moderate brown, conspicuous. Siphunculi concolorous with surrounding terga.

Cauda, anal, and subgenital plates concolorous with abdominal terga to subtly darker. Antennal segments V and IV subtly dusky distally, pale proximally, to entirely dusky, infrequently to moderate brown; III entirely very pale to subtly dusky on distal one-third, remainder pale; II as pale as proximal III to subtly darker; I concolorous with frons. Pro-, meso- and metatibiae concolorous, usually evenly pale, equivalent to thoracic tergum or slightly darker, to subtly dusky on distal and occasionally proximal tip, rarely entirely dusky. Distitarsi usually dusky on distal one-half, pale proximally, to entirely dusky with distal tip of tibiae.

Ultimate Stadium Nymphs of Viviparous Apterae.—Slide-mounted specimens: Nonmorphometrics as described for viviparous apterae except lacking body dorsum pigmentation suite; abdominal terga membranous with dorsal (major + minor) setae, between muscle attachment plates, arising from distinct scleroites. Mesonotum lacking 2 sclerotized plates extending from muscle attachment sites to engulf neighboring setal bases; area surrounding muscle attachment sites membranous.

Viviparous Alatae.—Slide-mounted specimens: Nonmorphometrics as described for viviparous apterae except lacking body dorsum pigmentation suite; abdominal terga normally membranous, dorsal setae between muscle attachment plates very rarely arising from distinct scleroites; antennal segments often as dark as tibiae, except proximal one-fifth of III pale. Antennal segment III with 0–5, IV with 0–3, secondary rhinaria. Epicranial suture strongly developed. Forewing medius with single furcation arising on proximad one-third of vein; cubital base arising proximad on subcosta with distance between anal and cubital bases on subcosta relatively small, ca. 20–30 percent or less of anal vein length; medius, especially cubitus and anal veins usually distinct, except infrequently proximad 10–15 percent vague. Abdominal terga lacking irregular sclerites that engulf or join muscle attachment plates and dorsal (major + minor) setal bases or scleroites.

Oviparae.—Slide-mounted specimens: Nonmorphometrics as described for viviparous apterae except abdominal dorsum membranous with irregular transverse sclerites containing dorsal (major + minor) setae on each tergum; marginal setae usually on separate scleroites; siphuncular cones sclerotized, regular, separated from other dorsal sclerotic fields; dorsal abdominal muscle attachment plates unicolorous. Rarely with abdominal terga II–VI sclerotic/fused, terga VII and VIII free; then dorsal demarcations of anterad terga evident and siphuncular cones surrounded closely by, sometimes engulfed by, sclerotic fields. Pseudorhinaria on metatibiae irregular, 11–23.

Males, Fundatrices.—Unknown.

Diagnosis.—*Essigella* (*E.*) *hoerneri* requires the combination of several characters for identification; individuals usually are pale and may be confused with other pale *Essigella*. *Essigella* (*E.*) *hoerneri* can be separated from all *Essigella*, except *E.* (*E.*) *californica* and *E.* (*E.*) *pini* by having six (Fig. 1F), instead of eight or more, dorsal (major + minor) setae on abdominal terga III–IV. Diagnostics for all morphs of *E.* (*E.*) *hoerneri* that separate it from *E.* (*E.*) *pini* are the same as for *E.* (*E.*) *californica* [see that diagnosis].

Essigella (*E.*) *hoerneri* and *E.* (*E.*) *californica* are difficult to distinguish. Although *E.* (*E.*) *hoerneri* has a longer rostrum, wider head and shorter antennal segment IV than does *E.* (*E.*) *californica*, these differences are indiscrete, and reliable separation requires application of the discriminant function in the key to the viviparous apterae [couplets 27 or 28, see 26].

Synonyms.—*Essigella gillettei* Hottes, NEW SYNONYM: holotype, vivip. alat., on slide alone; data: COLORADO. *LARIMER Co.*: Stove Prairie Hill, Bellevue, 16 Jun 1922, M. A. Palmer, *P. murrayana* [= *P. contorta latifolia*?]. *Essigella gillettei* holotype deposited in the NMNH.

Essigella maculata Hottes, NEW SYNONYM: holotype, vivip. alat., on slide alone; data: COLORADO. *MESA Co.*: Grand Junction, 2 Sep 1956, *Pinus edulis*. *Essigella maculata* holotype deposited in the NMNH.

Range.—Great Basin, from the Sierra Nevada to the Rocky Mountains, south of Idaho and Wyoming to Arizona, New Mexico and southern California; presumably into Mexico following its hosts (Fig. 9).
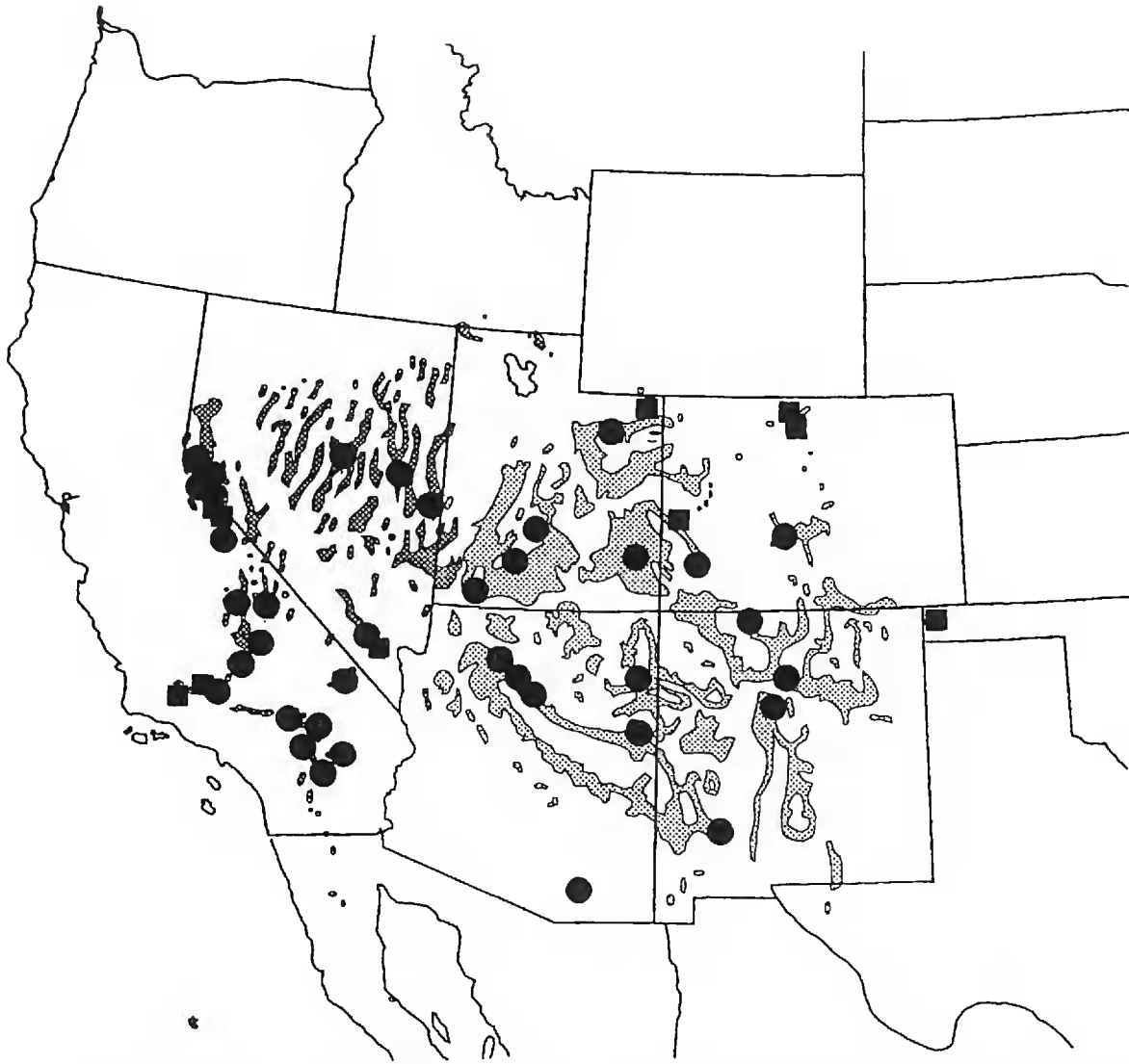
Figure 9.   Distribution of *E.* (*E.*) *hoerneri* [dots (JTS samples), squares (nonJTS samples)], super-imposed over the range of its hosts, *Pinus monophylla* [darker shading] and *Pinus edulis* [lighter shading (UT, AZ and east)].

Hosts. —*Pinus* section Parrya, subsection Cembroides: *P. edulis* Engelmann, *P. monophylla* Torrey & Frémont, *P. cembroides* Zuccagni and *P. quadrifolia* Par-latore [see discussion]. *Essigella* (*E.*) *hoerneri* is the only *Essigella* regularly on pinyon pines [*E.* (*L.*) *fusca* has rarely been taken on pinyons, but is considered nonresident]. References to *E.* (*E.*) *hoerneri* on *P. flexilis* and *P. ponderosa* are probably erroneous, or at least nonresident; although I have not yet seen the slides, I suspect they represent *E.* (*E.*) *californica,* or in the case of ponderosa pine possibly *E.* (*L.*) *fusca.*

Discussion. —*Essigella* (*E.*) *hoerneri* is closely related to *E.* (*E.*) *californica*; see the discussion of that species, where most comments apply equally to *E.* (*E.*) *hoerneri*]. The long rostrum and styli of *E.* (*E.*) *hoerneri* are autapomorphic; although, within other *Essigella* species complexes, some species may have these features slightly lengthened in comparison to their close relatives, that lengthening is not in the same class as here. In *E.* (*E.*) *hoerneri,* this appears to be an adaptation to feeding on pinyons, whose needles are relatively thick. Their needle thickness results from a failure to split into the multiple needles (Mirov 1967) that normally arise from a needle fascicle (e.g., *Pinus monophylla*). There is an east-west gradient for stylet length in this aphid, which appears to roughly reflect the needle diameter of the hosts. The more eastern populations of *E.* (*E.*) *hoerneri* (Colorado, New Mexico) have a relatively shorter rostrum, and the rostrum reaches maximal

relative length in the populations of the Owens Valley area of California, and western Nevada. This reflects their host pine geography and needle diameter: *Pinus monophylla,* a single-needled pinyon with a large diameter needle, occurs west of the Nevada-Utah border; whereas *P. edulis,* a double-needled pinyon with needles of proportionately less diameter, occurs to the east. The exact species status of these two pines may be questionable (W. B. Critchfield, personal communication).

Essigella (E.) hoerneri has apparently split (Fig. 13: node 10) from the *E. (E.) californica* lineage to ecologically reinvade *Pinus (Strobus),* on subsection Cembroides pines. These section Parrya pine niches are unoccupied by other *Essigella.* The *Archeoessigella* species feed monophagously within *Pinus (Strobus),* but in section Strobus, subsection Strobi; *E. (E.) californica* and *E. (E.) pini* also feed in that subsection in polyphagy; further, *E. (E.) californica* occurs on *P. albicaulis,* the sole Nearctic representative of *Pinus (Strobus)* section Strobus, subsection Cembrae. Interestingly, the other section Parrya subsections are not occupied by *Essigella:* subsection Gerardianae is Asian, but the Nearctic subsection Balfourianae probably predates *Essigella* (see Ecological Corroboration of *tĪ*).

Coded References to This Taxon. — *Essigella (E.) hoerneri* has been referred to previously by: the coding "Sp. B" (Sorensen 1983, 1987a, 1992b) and "HOER" in (Sorensen 1983), and by the name *E. hoerneri* in Sorensen (1983).

Etymology and Common Name. — This species was apparently named after J. L. Hoerner, who collected the series upon which the original description was based (Gillette & Palmer 1924: 5). Common name: Hoerner's pinyon pine needle aphid; although Palmer (1952: 15) refers to this species as "The Immaculate Pine Needle Aphid," the common name indicated here is more appropriate and less confusing because other *Essigella* are immaculate, in the sense of lacking "speckles" [see etymology for *E. (E.) pini*].

Material Examined. — ARIZONA. *APACHE Co.:* 5 km W of Eagar on hwy 273, 2140 m, 11 Sep 1978, JTS 78I15, *P. edulis,* (apt.); 6 km N of Lupton on hwy 12 (= 166), 1980 m, 11 Sep 1978, JTS 78I16, *P. edulis,* (apt., alat.). *COCHISE Co.:* Miller Canyon Rd, Huachuca Mts, 1700 m, 17 Sep 1978, JTS 78I53, *P. cembroides,* (apt.). *COCONINO Co.:* 22 km N of Williams on hwy 64, 2070 m, 9 Sep 1978, JTS 78I7, *P. edulis,* (apt.); 32 km S of Grand Canyon Village on hwy 180, 2070 m, 9 Sep 1978, JTS 78I9, *P. edulis,* (apt.); 8 km W of Grand Canyon Caverns on hwy 60, 1700 m, 9 Sep 1978, JTS 78I3, *P. edulis,* (apt.). CALIFORNIA. *INYO Co.:* Bristlecone Pine Forest entrance on hwy 168, Inyo Natl Forest, W of Westgard Pass, 2230 m, 31 Jul 1977, JTS 77G74, *P. monophylla,* (apt.); jct of Lake Sabrina Rd & Southern Calif. Edison Plant 2 Rd, nr Bishop, 2130 m, 1 Aug 1977, JTS 77H3, *P. monophylla,* (apt., alat.). *KERN Co.:* Valle Vista Cmpgd, 13 km W of Apache Saddle Ranger Station, 1500 m, 18 Sep 1977, JTS 77I56, *P. monophylla,* (apt.); W side of Walker Pass on hwy 178, 26 km E of Oyx, 1530 m, 20 Sep 1977, JTS 77I63, *P. monophylla,* (apt., alat.). *MONO Co.:* Cedar Flat, nr White Mt, 15 Jul 1961, E. I. Schlinger, EIS 61-7-15h, "Pinon pine," (apt.); E side of Monitor Pass on hwy 89, 2070 m, 17 Jul 1977, JTS 77G36, *P. monophylla,* (apt., alat.); Lee Vining Cmpgd, Inyo Natl Forest, W of Tioga Pass on hwy 120, 2290 m, 31 Jul 1977, JTS 77G70, *P. monophylla,* (apt.); Sherwin Summit, 17 Jul 1972, D. J. Voegtlin, DJV 47, *P. monophylla,* (apt.); Topaz Lake, 1680 m, 5 Jul 1979, S. Paulaitis, DJV 541, *P. monophylla,* (apt.). *RIVERSIDE Co.:* 2 km N of Paradise Valley on hwy 74, 1500 m, 9 Sep 1977, JTS 77I19, *P. quadrifolia,* (apt.); Alpine Village, 21 km S of Palm Desert on hwy 74, 1160 m, 9 Sep 1977, JTS 77I17, *P. monophylla,* (apt.); Joshua Tree Natl Monument, Key's View, 1530 m, 12 Sep 1977, JTS 77I33, *P. monophylla,* (apt.). *SAN BERNARDINO Co.:* 16 km W of Barton Flat on hwy 38, 2140 m, 16 Sep 1977, JTS 77I40, *P. monophylla,* (apt.); Pipes Cyn, NW of Yucca Valley & Pioneer Town, 8 km NW of jct of Pioneertown Rd & Pipes Canyon Rd, 1530 m, 15 Sep 1977, JTS 77I34, *P. monophylla,* (apt., alat.); Sheep Cyn, 2 km NW of Mountain Top Jct on hwy 138, 1525 m, 17 Sep 1977, JTS 77I47, *P. monophylla,* (apt.); nr Ivanpah, New York Mts,

1600 m, 8 Sep 1978, JTS 78I2, *P. monophylla,* (apt.); same but 1700 m, JTS 78I1, *P. edulis,* (apt.). *VENTURA Co.:* Cuyama Valley, 22 May 1959, E. I. Schlinger, EIS 59-5-23i, *P. "cembroides"* [?], (apt., alat.); Lake of the Woods, 10 km W of Tejon Pass, 1556 m, 18 Sep 1977, JTS 77I53, *P. monophylla,* (apt., alat.). *COUNTY UNCERTAIN:* Frazier Park, 22 May 1959, E. I. Schlinger, EIS 59-5-23d, *P. "cembroides"* [?], (apt., alat.) (slide is labeled "Los Angeles" Co., but Frazer Park is in Kern Co.; however, main roads in NW L.A. Co. are less than ~5 km away and Ventura Co. is also immediately adjacent). COLORADO. *CHAFFE Co.:* Poncha Springs, 2440 m, 12 Aug 1978, JTS 78H69, *P. edulis,* (apt.). *LARIMER Co.:* (lectotype) Owl Cyn, 25 Sep 1921, C. P. Gillette & J. Hoerner, CAES 2894, *P. edulis,* (apt.); (paratype) same but 10 Oct 1921, C. L. Corkins, CAES 3028/USNM 41952, (apt., ovip.); (paratype) same but 6 Nov 1921, J. Hoerner, CAES 3035, (ovip.). *MESA Co.:* Grand Junction, 2 Sep 1956, *P. edulis,* (alat.); same but 3 Oct 1956, F. C. Hottes, (alat.). *SAN MIGUEL Co.:* 6 km NE of Placerville on hwy 62, 2320 m, 7 Aug 1978, JTS 78H41, *P. edulis,* (apt.). *COUNTY UNCERTAIN:* Refe, 17 Aug 1956, *P. edulis,* (apt.). NEVADA. *CLARK Co.:* Charleston Mts, Lee Canyon Rd (hwy 52), 2290 m, 4 Aug 1978, JTS 78H14, *P. monophylla,* (apt.); same but Lee Canyon Ski Area, 2590 m, JTS 78H18, *P. ponderosa,* (alat.); W of Las Vegas, 20 Apr 1978, C. F. Smith, CFS 78-56, *P. monophylla,* (apt., alat.). *DOUGLAS Co.:* hwy 395, 16 km NW of jct with hwy 3, Pine Nut Mts, 1650 m, 16 Jul 1977, JTS 77G35, *P. monophylla,* (apt.). *LANDER Co.:* Scott Summit on hwy 50, 11 km E of Austin, 2230 m, 26 Aug 1978, JTS 78H158, *P. monophylla,* (apt., alat.). *WASHOE Co.:* Mt Rose, Slide Mountain Ski Area, 2 Aug 1978, JTS 78H6, *P. washoensis,* (alat.). *WHITE PINE Co.:* Leyland Cave Natl Monument, 2074 m, 26 Aug 1978, JTS 78H156, *P. monophylla,* (apt.); Little Antelope Summit on hwy 50, 56 km E of Eureka, 2260 m, 26 Aug 1978, JTS 78H157, *P. monophylla,* (apt.). NEW MEXICO. *BERNALILLO Co.:* Crest View, hwy 14, 2280 m, 12 Sep 1978, JTS 78I21, *P. edulis,* (apt., alat., ovip.). *RIO ARRIBA Co.:* 8 km S of Tierra Amarilla on hwy 84, 2410 m, 8 Aug 1978, JTS 78H52, *P. edulis,* (apt., alat.). *SANTA FE Co.:* 20 km NE of Santa Fe on hwy 475, 2680 m, 10 Aug 1978, JTS 78H57, *P. edulis,* (apt.). *SIERRA Co.:* 2 km E of Kingston on hwy 90, 1860 m, 14 Sep 1978, JTS 78I31, *P. edulis,* (apt.). OKLAHOMA. *CIMARRON Co.:* Kenton, 16 May 1961, Van Cleave, "Pinon pine," (apt., alat.). UTAH. *DAGGETT Co.:* Flaming Gorge Dam, Dutch John, 22 Jun 1978, C. S. Smith, CFS 78-238, "pinyon pine," (apt., alat.) (slides of this series marked Butch John and Dutch John, Wyoming). *DUCHESNE Co.:* Starvation lake, hwy 40, 1800 m, 25 Aug 1978, JTS 78H140, *P. edulis,* (apt.). *GARFIELD Co.:* hwy 20, 5 km W of jct with hwy 89, 2040 m, 6 Aug 1978, JTS 78H32, *P. edulis,* (apt.). *SEVIER Co.:* 35 km E of Salina on hwy 70, 2130 m, 6 Aug 1978, JTS 78H33, *P. edulis,* (apt., alat.). *WASHINGTON Co.:* 43 km SW of Cedar City on hwy 15, 1220 m, 5 Aug 1978, JTS 78H22, *P. monophylla,* (apt.). *WAYNE Co.:* 2 km NE of La Sal on hwy 46, 2230 m, 6 Aug 1978, JTS 78H36, *P. edulis,* (apt.).

Essigella (Essigella) wilsoni Hottes, 1957

Essigella wilsoni Hottes, 1957: 106, Proc. Biol. Soc. Wash., 70: 106–108.

Essigella pergandei Hottes, 1957: 100, Proc. Biol. Soc. Wash., 70: 100. NEW SYNONYM.

Essigella oregonensis Hottes, 1958: 155, Proc. Biol. Soc. Wash., 71: 155–156. NEW SYNONYM.

Primary Type. —Holotype, vivip. apt., on slide with 6 other specimens, holotype shown by arrows (12 o'clock position); data: "Douglas Fir, Whitby Isd., Seattle, Wash., Aug 29, 1955, M. J. Forsell, Coll./Holotype, *Essigella wilsoni* F.C. Hottes" (reference to "Whitby Isd." may be to "Whidbey Island" in Island Co.; Seattle is in King Co.). Holotype deposited in the Essig Museum of Entomology, University of California at Berkeley, Berkeley, California.

Viviparous Apterae. —*Morphology:* Body length: 1.24–2.03 (1.49 ± 0.22) mm. HEAD: Primary rhinarium on terminal antennal segment (V) exceptionally distad, distance from tip of processus terminalis to distal face of rhinarial rim less than 0.5, usually 0.3,× diameter of rhinarium; distal face of rhinarial rim usually perpendicular to longitudinal axis of antennal segment; rhinarial membrane usually conspicuously protuberant. Length of antennal segment V: 83–113 (101 ± 8) μ, processus terminalis: 20–40 (31 ± 5) μ; IV: 66–95 (82 ± 9) μ; III: 83–183 (133 ± 23) μ; II: 55–80 (66 ± 6) μ.
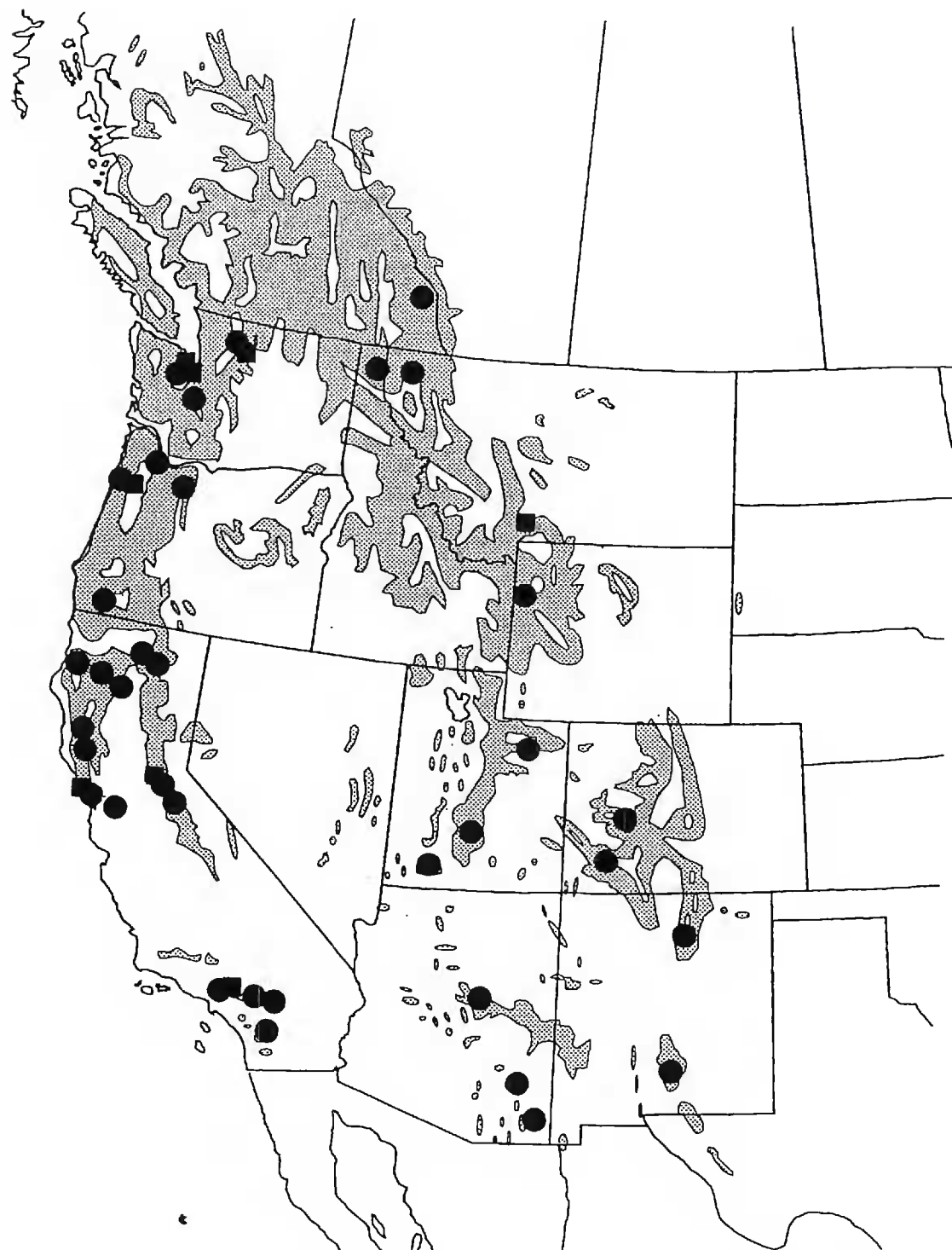
Figure 10.   Distribution of *E. (E.) wilsoni* [dots (JTS samples), squares (nonJTS samples)], superimposed over the range of its hosts, *Pseudotsuga menzeisii* [darker shading] and *Pseudotsuga macrocarpa* [lighter shading (Santa Barbara Co. and south in CA)].

Length of longest setae on frons: 13–35 (22 ± 6) μ, tips incrassate to sharp. Head width: 225–286 (248 ± 14) μ. Length of stylets: 408–653 (525 ± 64) μ; ultimate rostral segment: 43–73 (64 ± 7) μ, rostral tip reaching abdominal terga I–II, infrequently III, in dorsal view through slide-mounted specimens. Head + pronotum fused, total length: 281–428 (332 ± 37) μ. THORAX: Meso + metanota fused, total length: 204–357 (265 ± 35) μ. ABDOMEN: Tergum I free, length: 71–153 (99 ± 20) μ; terga II–VII fused, VIII free. Maximum distal width of flange on siphunculi: 31–48 (38 ± 5) μ; siphunculi flush to truncated conical, protruding to 0.5× maximal distal width. Ventral abdominal sclerites on segments III–IV usually irregular, subcircular when small (length less than 0.6× metatibial diameter), to subquadrate when large (length greater than 1.0× metatibial diameter); length: 5–53 (27 ± 15) μ, 0.1–1.3× diameter of metatibiae. Dorsal (major + minor) setae (see Fig. 1E) on abdominal terga III–IV: usually 8, occasionally 10, very rarely 12, tips sharp, when 8 setae then in 1 row, infrequently single mesad or lateral-most minor dorsal seta anterad, when 10 or more then in 2 irregular rows, usually with lateral-most minor dorsal seta on each side anterad to its next mesad neighbor; marginal setae 2 per segment, each side. Setae on abdominal tergum VIII: 6, rarely to 8, length: 8–28 (12 ± 5) μ, tips incrassate to sharp, in 1 row. Cauda rounded; caudal protuberance

moderately to poorly developed, infrequently absent; length of longest caudal setae: 45–88 (58 ± 11) μ, tips sharp. LEGS: Length of metafemora: 393–592 (466 ± 52) μ; metatibiae: 561–836 (682 ± 78) μ; longest dorsal setae on central one-third of metatibiae: 10–35 (18 ± 7) μ, 0.05–1.5× diameter of metatibiae, tips incrassate to sharp; approximately equal or very gradually increasing distally, no setal length dimorphism; longest ventral setae on metatibiae: 15–38 (24 ± 6) μ, tips sharp. Length of metabasitarsus: 79–110 (94 ± 8) μ; metadistitarsus: 125–180 (155 ± 16) μ. Ratio of metadistitarsus to metabasitarsus less than 1.9:1, mean 1.65:1. *Pigmentation:* Color in life: Lime green throughout. Slide-mounted specimens: Background of body dorsum pale (to 10 percent pigment density), unicolorous. Terga at bases of setae on frons and dorsal (major + minor) setae on abdomen concolorous with surrounding terga. Thoracic muscle attachment plates and dorsal muscle attachment plates of abdomen pale, inconspicuous. Spiracular plates and ventral abdominal sclerites pale to infrequently light brown. Siphunculi concolorous with surrounding terga. Cauda, anal and subgenital plates pale, concolorous with abdominal terga, to subtly darker. Antennal segments V and IV dusky, concolorous; III entirely pale, to distal one-half dusky, remainder pale; II concolorous with proximal III; I concolorous with frons, to subtly darker. Pro-, meso- and metatibiae usually pale, concolorous and equivalent to body dorsum, infrequently entire tibiae slightly dusky, subtly darker than body dorsum. Distitarsi entirely pale to subtly dusky on distal one-third.

Ultimate Stadium Nymphs of Viviparous Apterae. — Slide-mounted specimens: Nonmorphometrics as described for viviparous apterae except lacking body dorsum pigmentation suite; abdominal terga membranous with dorsal (major + minor) setae, between muscle attachment plates, arising from distinct scleroites. Mesonotum lacking 2 sclerotized plates extending from muscle attachment sites to engulf neighboring setal bases; area surrounding muscle attachment sites membranous.

Viviparous Alatae. — Slide-mounted specimens: Nonmorphometrics as described for viviparous apterae except lacking body dorsum pigmentation suite; abdominal terga normally membranous, dorsal (major + minor) setae between muscle attachment plates occasionally arising from distinct scleroites; antennal segments often as dark as tibiae, except proximal one-fifth of III pale. Antennal segment III with 1, IV with 0, secondary rhinaria. Epicranial suture absent to vaguely developed. Forewing medius with single furcation arising on proximad one-third of vein; cubital base usually arising distad, infrequently proximad, on subcosta with distance between anal and cubital bases on subcosta usually relatively large, ca. 30–40 percent or more of anal vein length; medius, especially cubitus and anal veins distinct, except infrequently proximad 10–15 percent vague. Abdominal terga lacking irregular sclerites that engulf or join muscle attachment plates and dorsal (major + minor) setal bases or scleroites.

Oviparae. — Slide-mounted specimens: Nonmorphometrics as described for viviparous apterae except abdominal dorsum membranous with faint, irregular transverse sclerites containing dorsal (major + minor) setae on each tergum; marginal setae usually on separate faint scleroites; siphuncular cones sclerotized, regular, separated from other dorsal sclerotization fields; dorsal abdominal muscle attachment plates faint, unicolorous. Pseudorhinaria on metatibiae irregular, 9–15.

Males, Fundatrices. — Unknown.

Diagnosis. — *Essigella* (*E.*) *wilsoni* can be identified by the unique primary rhinarium that is unusually protuberant and exceptionally close to the tip of the antennal segment V. This species is pale.

Synonyms. — *Essigella oregonensis* Hottes, NEW SYNONYM: holotype, vivip. apt., on slide with 1 male; data: OREGON. *CLACKAMAS Co.:* Government Camp, 17 Aug 1957, *Pinus albicaulis. Essigella oregonensis* holotype deposited in the NMNH.

Essigella pergandei Hottes, NEW SYNONYM: holotype, vivip. apt., several specimens on slide, holotype circled; data: WASHINGTON. *KING Co.:* Seattle, 17 Jul 1955, M. J. Forsell, *"Abies concolor"* (Gordon) Lindberg [reference to *"Abies concolor"* presumably is a mistaken identification of *Pseudotsuga menziesii,* see host discussion below]. *Essigella pergandei* holotype deposited in the NMNH.

Range. — Southern British Columbia and Alberta, throughout the western U.S. (exclusive of Alaska), presumably south into Mexico as far as its hosts (Fig. 10).

Hosts.—*Pseudotsuga menziesii* (Mirbel) Franco and *Pseudotsuga macrocarpa* (Vasey) Mayr. Many museum slides (other collectors), are labeled *Abies concolor* (e.g., *E. pergandei* holotype), or simply "fir." Also, there is one record (*E. oregonensis* holotype) from *Pinus albicaulis,* which is probably opportunistic. *Essigella* (*E.*) *wilsoni* is a commonly collected species that has transferred exclusively to a host other than *Pinus.* Numerous records from *Abies* are most probably in error; my extensive sampling (Sorensen 1983) on *Abies* did not yield any *Essigella.* Whenever I sampled *E.* (*E.*) *wilsoni* from what I thought to be an *Abies,* there was invariably an adjacent *Pseudotsuga* with a branch intermingled that proved to be the host. If *Abies* is a host, it is very much less commonly used than *Pseudotsuga.*

Discussion.—*Essigella* (*E.*) *wilsoni* is common and morphologically homogeneous. The condition of the primary rhinarium on antennal segment V is an autapomorphy. Its other apomorphies are listed in the discussion of *E.* (*E.*) *californica.* The length of dorsal setae on the metatibiae varies somewhat similarly to, but not to the extent of, *E.* (*E.*) *californica.*

The male of *E.* (*E.*) *wilsoni* is unknown. The morphotype male [synonym *E. pergandei*] is too poorly mounted and positioned to determine its species; its primary rhinarium is not characteristic of *E.* (*E.*) *wilsoni,* and it may be a male *E.* (*E.*) *californica.* The rhinarial difference may be a sexual character difference or preparation artifact, however?

The phylogenetic placement of *E.* (*E.*) *wilsoni* is confusing; see alternative analyses in the phylogenetics section. Ordinations (Sorensen 1992b) place it closest to *E.* (*E.*) *pini* and *E.* (*E.*) *essigi* in discriminant space, but conventional (coded data) cladistic analyses suggest it forms a trichotomy with the *E.* (*E.*) *californica* clade and series B (unpublished data). On the basis of many bivariant regression plottings (unpublished data), I feel *E.* (*E.*) *wilsoni* shows the closest relationship to the *E.* (*E.*) *californica* complex. Many traits that I discount as homoplasies suggest a relationship to *E.* (*E.*) *alyeska*; however, I believe the broad body of the latter is a strong synapomorphy linking it to the *E.* (*E.*) *knowltoni* complex, as is its host association.

Coded References to This Taxon.—*Essigella* (*E.*) *wilsoni* has been referred to previously by: the coding "Sp. C" (Sorensen 1983, 1987a, 1992b) and "WILS" (Sorensen 1983), and by the name *E. wilsoni* in Sorensen (1983).

Etymology and Common Name.—Hottes (1957: 107) named this species after aphidologist H. F. Wilson, who described the second named *Essigella* species, *E.* (*E.*) *pini.* Hottes apparently attributed the naming to Wilson's (1919: 1) mention of "*E. californica* (Essig)" from *Pseudotsuga* "*douglasii*" [= *P. menziesii*]. He probably (correctly) deduced, from mention of that host, that his own "*E. wilsoni*" was involved, because Hottes undoubtedly could not make such a deduction from the description or characters mentioned by Wilson. Common name: Wilson's Douglas fir needle aphid.

Material Examined.—ARIZONA. *COCHISE Co.:* nr Rustler park, Chiricahua Mts, 2500 m, 16 Sep 1978, JTS 78I51, *Pseudotsuga menziesii,* (apt.). *GILA Co.:* 32 km E of Kohles Ranch on hwy 260, 10 Sep 1978, JTS 78I12, *Pseudotsuga menziesii,* (apt.). *GRAHAM Co.:* 34 km SW of Stafford

on hwy 366, 2170 m, 15 Sep 1978, JTS 78I41, *Pseudotsuga menziesii,* (apt.). CALIFORNIA. *EL DORADO Co.:* Blodgett Experimental Forest (Univ. Calif.), E of Georgetown, 26 Jul 1973, D. J. Voegtlin, DJV 57, *Pseudotsuga menziesii,* (apt.); same but 28 Apr 1977, J. T. Sorensen, (apt.). *HUM-BOLT Co.:* Lord Ellis Summit on hwy 299, W of Willow Creek, 670 m, 21 Aug 1977, JTS 77H25, *Pseudotsuga menziesii,* (apt.). *LAKE Co.:* 18 km W of Lake Pillsbury, Eel River Rd, 490 m, 24 Jul 1977, JTS 77G55, *Pseudotsuga menziesii,* (apt.). *LOS ANGELES Co.:* hwy 2, 15 km NE of jct with hwy 39, San Gabriel Mts, 2290 m, 17 Sep 1977, JTS 77I50, *Pseudotsuga macrocarpa,* (apt.). *MARIN Co.:* Alpine Lake, 25 Mar 1977, J. T. Sorensen, *Pseudotsuga menziesii,* (apt.); Muir Woods, 27 Mar 1964, C. F. Smith & Graham, CFS 64-27, *"Abies"* [assumed erroneous], (apt.). *MENDOCINO Co.:* Fish Rock Rd, 27 km E of hwy 1, 490 m, 23 Jul 1977, JTS 77G50, *Pseudotsuga menziesii,* (apt.); Nature Conservancy Coastal Redwood Preserve, 8 km N of Branscomb, 13 May 1978, JTS 78E103, *Pseudotsuga menziesii,* (apt.). *PLUMAS Co.:* Jackson Creek Cmpgd, Plumas Natl Forest, 2 km SE of Cromberg on hwy 70/89, 1280 m, 26 Jun 1977, JTS 77F11, *Pseudotsuga menziesii,* (apt.). *SAN BERNARDINO Co.:* 3 km NE of Lake Gregory Village, San Bernardino Mts, 1310 m, 17 Sep 1977, JTS 77I46, *Pseudotsuga macrocarpa,* (apt.); 8 km W of Barton Flat on hwy 38, 1920 m, 16 Sep 1977, JTS 77I37, *Pseudotsuga macrocarpa,* (apt.). *SAN DIEGO Co.:* Mt Palomar Rd (S6), 5 km S of Mt Palomar, 1370 m, 11 Sep 1977, JTS 77I26, *Pseudotsuga macrocarpa,* (apt.). *SISKIYOU Co.:* Deadhorse Summit on hwy 89, 10 km SE of Bartel, 1370 m, 3 Jul 1977, JTS 77G11, *Pseudotsuga menziesii,* (apt.); Mt Shasta Ski Bowl Rd, 2450 m, 2 Jul 1977, JTS 77G7, *Pseudotsuga menziesii,* (apt.). *TEHAMA Co.:* 45 km E of Dales on hwy 36, 1460 m, 10 Jul 1977, JTS 77G26, *Pseudotsuga menziesii,* (apt.). *TRINITY Co.:* 3 km W of Weaverville on hwy 299, 730 m, 20 Aug 1977, JTS 77H22, *Pseudotsuga menziesii,* (apt.); Buckhorn Summit on hwy 299, W of Tower House, 980 m, 20 Aug 1977, JTS 77H18, *Pseudotsuga menziesii,* (apt.); Ironside Mt Lookout Rd, W of Junction City, 1070 m, 21 Aug 1977, JTS 77H24, *Pseudotsuga menziesii,* (apt.). *TUOLUMNE Co.:* Yosemite Natl Park, hwy 120 entrance, 1700 m, 1 Aug 1977, JTS 77H7, *Pseudotsuga menziesii,* (apt.). *VENTURA Co.:* 5 km NNE of Pine Mt Summit on hwy 33, 1340 m, 19 Sep 1977, JTS 77I57, *Pseudotsuga macrocarpa,* (apt.); Pine Mt Summit, 16 May 1961, R. Van den Bosch & J. Hall, RVdB 61-V-19L, "white fir" [assumed erroneous], (apt.). COLORADO. *GUNNISON Co.:* 16 km NW of Kebler Pass, 2440 m, 13 Aug 1978, JTS 78H76, *Pseudotsuga menziesii,* (apt.). *SAN MIGUEL Co.:* 6 km NE of Placerville on hwy 62, 2320 m, 7 Aug 1978, JTS 78H42, *Pseudotsuga menziesii,* (apt.). IDAHO. *BONNER Co.:* 6 km S of Cocolalla on hwy 95, 18 Jul 1978, JTS 78G106, *Pseudotsuga menziesii,* (apt.). MONTANA. *GALLATIN Co.:* Battle Ridge Pass, Bridger Mts, S of Bozeman, 19 Aug 1979, D. J. Voegtlin, DJV 702, *Pseudotsuga menziesii,* (apt.). *LINCOLN Co.:* 4 km S of Stryker on hwy 93, nr Flathead Co. line, 17 Jul 1978, JTS 78G96, *Pseudotsuga menziesii,* (apt.). NEW MEXICO. *OTERO Co.:* 3 km W of Cloudcroft on hwy 82, 2560 m, 13 Sep 1978, JTS 78I24, *Pseudotsuga menziesii,* (apt.). *SANTA FE Co.:* 30 km NE of Santa Fe on hwy 475, 3110 m, 10 Aug 1978, JTS 78H54, *Pseudotsuga menziesii,* (apt.). OREGON. *BENTON Co.:* Corvallis, 25 Jan 1915, L. Childs, *Pseudotsuga menziesii,* (apt.). *CLACKAMAS Co.:* Government Camp, 17 Aug 1958, *P. albicaulis,* (ovip.). *JOSEPHINE Co.:* O'brien, 4 Jul 1978, JTS 78G10, *Pseudotsuga menziesii,* (apt.). *POLK Co.:* 6 km W of Grand Ronde on hwy 18, 7 Jul 1978, JTS 78G41, *Pseudotsuga menziesii,* (apt.). *WASCO Co.:* 46 km SE of Government Camp on hwy 26, 670 m, 6 Jul 1978, JTS 78G30, *Pseudotsuga menziesii,* (apt.). *WASHINGTON Co.:* 21 km W of Manning on hwy 26, 7 Jul 1978, JTS 78G48, *Pseudotsuga menziesii,* (apt.). UTAH. *DUCHESNE Co.:* 19 km NE of Castle Lake on hwy 33, 2780 m, 25 Aug 1978, JTS 78H146, *Pseudotsuga menziesii,* (apt.). *IRON Co.:* 16 km SE of Cedar City on hwy 14, 2170 m, 5 Aug 1978, JTS 78H23, *Pseudotsuga menziesii,* (apt.). *SEVIER Co.:* 66 km E of Salina on hwy 70, 2227 m, 6 Aug 1978, JTS 78H34, *Pseudotsuga menziesii,* (apt.). WASHINGTON. *KING Co.:* Seattle, 17 Jul 1955, J. W. Forsell, *"Abies concolor"* [assumed erroneous], (apt.); same but 25 Apr 1973, D. Pike, *Pseudotsuga menziesii,* (apt.). *KITSAP Co.:* 8 km S of Hood Canal bridge on hwy 3, 9 Jul 1978, JTS 78G50, *Pseudotsuga menziesii,* (apt.). *OKANOGAN Co.:* 17 km NW of Winthrop on hwy 20, 550 m, 12 Jul 1978, JTS 78G72, *Pseudotsuga menziesii,* (apt.); Loup Loup Pass, Okanogan Natl Forest, 19 Sep 1979, D. J. Voegtlin, DJV 759, *Pseudotsuga menziesii,* (apt.). *PIERCE Co.:* hwy 706, nr Ashford, 11 Jul 1978, JTS 78G57, *Pseudotsuga menziesii,* (apt., alat.). *COUNTY UNCERTAIN:* [see primary type paragraph] (type) "Whitby Island," "Seattle," 29 Aug 1955, M. J. Forsell, (apt.). WYOMING. *TETON Co.:* 35 km SE of Jackson on hwy 187, 1950 m, 23 Aug 1978, JTS 78H130, *Pseudotsuga menziesii,* (apt.). CANADA. *BRITISH CO-LUMBIA:* 35 km S of Radium Hot Springs on hwy 93, 17 Jul 1978, JTS 78G90, *Pseudotsuga menziesii,* (apt.).

Series B

Essigella (Essigella) alyeska Sorensen, 1988

Essigella alyeska Sorensen, 1988: 118, Pan-Pacif. Entomol., 64: 118–121.
Essigella "alyeska" Sorensen, 1983: 112 (unpublished manuscript name) Ph.D.
Thesis, University of California at Berkeley, Berkeley, California. 605 p.

Type Series. —Holotype, vivip. apt., on slide with 1 paratype vivip. apt., holotype on top (12 o'clock position); data: ALASKA. *FAIRBANKS NORTH STAR BOROUGH:* College (Univ. Alaska campus), nr Fairbanks, 24 Jun 1979, J. T. Sorensen (79F1), *Picea glauca.* Holotype retained in Sorensen collection, eventually to be deposited in The Natural History Museum, London. Paratypes (all same data as holotype): 25 vivip. apt. on 13 slides including holotype slide. Paratype slides deposited: 1 slide in NMNH, Washington, D.C.; 1 slide in CNC, Ottawa, Ontario; 11 slides in Sorensen collection.

Viviparous Apterae.—Morphology: Body length: 1.42–1.65 (1.51 ± 0.07) mm. HEAD: Primary rhinarium on terminal antennal segment (V) not exceptionally distad, distance from tip of processus terminals to distal face of rhinarial rim greater than 0.5× diameter of rhinarium; distal face of rhinarial rim usually oblique to longitudinal axis of antennal segment; rhinarial membrane not conspicuously protuberant. Length of antennal segment V: 100–120 (108 ± 8) μ, processus terminalis: 28–38 (34 ± 4) μ; IV: 83–98 (86 ± 5) μ; III: 138–170 (151 ± 11) μ; II: 63–73 (67 ± 3) μ. Length of longest setae on frons: 33–53 (41 ± 7) μ, tips incrassate, rarely sharp. Head width: 286–301 (292 ± 301) μ. Length of stylets: 561–775 (600 ± 69) μ; ultimate rostral segment: 63–85 (74 ± 8) μ, rostral tip reaching abdominal terga I–II in dorsal view through slide-mounted specimens. Head + pronotum fused, total length: 337–388 (361 ± 16) μ. THORAX: Meso + metanota fused, total length: 265–316 (298 ± 17) μ. ABDOMEN: Tergum I free, length: 102–118 (108 ± 7) μ; terga II–VII fused, VIII free. Maximum distal width of flange on siphunculi: 43–48 (46 ± 2) μ; siphunculi strongly protuberant, protruding 0.7–1.1× maximal distal width. Ventral abdominal sclerites on segments III–IV irregular, to subcircular when large; length: 26–40 (35 ± 5) μ, 0.8–1.4× diameter of metatibiae. Dorsal (major + minor) setae (see Fig. 1E) on abdominal terga III–IV: 7–9, usually 8, tips sharp, in 1 row; marginal setae 2 each side, per segment. Setae on abdominal tergum VIII: 6–8, length: 15–45 (36 ± 10) μ, tips incrassate to sharp, in 1 row. Cauda broadly rounded; caudal protuberance poorly developed to absent; length of longest caudal setae: 83–100 (91 ± 7) μ, tips sharp. LEGS: Length of metafemora: 428–520 (488 ± 33) μ; metatibiae: 663–785 (731 ± 44) μ; longest dorsal setae on central one-third of metatibiae: 30–45 (38 ± 5) μ, 0.7–1.5× diameter of metatibiae, tips incrassate, rarely sharp; approximately equal or very gradually increasing distally, no setal length dimorphism; longest ventral setae on metatibiae: 23–33 (28 ± 7) μ, tips sharp. Length of metabasitarsus: 95–103 (99 ± 2) μ; metadistitarsus: 135–158 (147 ± 8) μ. Ratio of metadistitarsus to metabasitarsus less than 1.9:1, mean 1.48:1. *Pigmentation:* Color in life: Body gray-green, head yellow-orange. Slide-mounted specimens: Background of body dorsum pale to light brown (to 20 percent pigment density), unicolorous. Terga at bases of setae on frons and dorsal (major + minor) setae on abdomen concolorous with surrounding terga. Thoracic muscle attachment plates and dorsal muscle attachment plates of abdomen pale, inconspicuous, to moderate brown, conspicuous. Spiracular plates and ventral abdominal sclerites pale, to dark brown, conspicuous. Siphunculi concolorous with surrounding terga, to subtly darker, especially distally near flange. Cauda, anal and subgenital plates light to moderate brown, subtly to substantially darker than abdominal terga. Antennal segments V and IV light to moderate brown, IV sometimes proximally pale; III pale if proximal IV pale, to dusky on distal one-half, if IV entirely darker; II subtly darker than proximal III: I as dark as V, or nearly so, and subtly darker than frons. Pro-, meso- and metatibiae usually concolorous, pale, equivalent to body dorsum, sometimes slightly dusky on distal tip, entire tibiae infrequently slightly darker. Distitarsi entirely dusky.

Ultimate Stadium Nymphs of Viviparous Apterae. —Slide-mounted specimens: Nonmorphometrics as described for viviparous apterae except lacking body dorsum pigmentation suite; abdominal terga membranous with dorsal (major + minor) setae, between muscle attachment plates, arising from distinct scleroites. Mesonotum lacking 2 sclerotized plates extending from muscle attachment sites to engulf neighboring setal bases; area surrounding muscle attachment sites membranous.

Viviparous Alatae. —Slide-mounted specimens: Nonmorphometrics as described for viviparous ap-

terae except lacking body dorsum pigmentation suite; abdominal terga normally membranous, dorsal (major + minor) setae between muscle attachment plates sometimes arising from distinct scleroites; antennal segments often as dark as tibiae, except proximal one-fifth of III pale. Antennal segment III with 0–2, IV with 0, secondary rhinaria. Epicranial suture absent to weakly developed. Forewing medius with furcation arising on central one-third of vein; cubital base usually arising distad, uncommonly proximad, on subcosta with distance between anal and cubital bases on subcosta usually relatively large, ca. 20–40 percent or more of anal vein length; medius, especially cubitus and anal veins usually distinct, except infrequently proximad 10–15 percent vague. Abdominal terga lacking irregular sclerites that engulf or join muscle attachment plates and dorsal (major + minor) setal bases or scleroites.

Oviparae, Males, Fundatrices. —Unknown.

Diagnosis. —*Essigella* (*E.*) *alyeska* requires the combination of several characters for identification, because it may be confused with other pale *Essigella*. *Essigella* (*E.*) *alyeska* can be separated from *E.* (*E.*) *californica, E.* (*E.*) *hoerneri* and *E.* (*E.*) *pini* by having eight (Fig. 1E), rather than six, dorsal (major + minor) setae on abdominal terga III–IV. It can be distinguished from *E.* (*A.*) *kathleenae, E.* (*A.*) *kirki, E.* (*L.*) *eastopi, E.* (*L.*) *fusca* and *E.* (*L.*) *hillerislambersi* by having two, instead of three or usually more, marginal setae on abdominal terga III–IV, and having small and noninvasive, rather than large and invasive, mesonotal muscle attachment plates on later stadia nymphs of apterae. *Essigella* (*E.*) *alyeska* lacks the thoracic fusion of *E.* (*E.*) *essigi*, and the protuberant, exceptionally distad primary rhinarium of *E.* (*E.*) *wilsoni*. Some individuals of *E.* (*E.*) *alyeska* are particularly similar to small, pale *E.* (*E.*) *critchfieldi* and *E.* (*E.*) *knowltoni* [especially *E.* (*E.*) *knowltoni braggi*], but differ from these by often having: often small, instead of always large, ventral abdominal sclerites on segments III–IV; two, instead of three or four, marginal setae on abdominal terga III–IV; and small and noninvasive, rather than large and invasive, mesonotal muscle attachment plates on later stadia nymphs of apterae.

Range. —Interior of Alaska, Ontario and Quebec (Fig. 11) [known only from the type series and three other collections]. I anticipate that *E.* (*E.*) *alyeska* will be found in the northern Rocky Mountains in the U.S., and across Canada, wherever the hosts occur.

Hosts. —*Picea glauca* (Moench) Voss, *Pinus banksiana* Lambert. Collections of *E.* (*E.*) *alyeska* are too few to reliably suggest which host is usual. My extensive sampling of *Picea* and all other conifers in Alaska, beyond the northern limits of *Pinus*, yielded *E.* (*E.*) *alyeska* in only two locations; it was not found during extensive samplings of all conifers in the western U.S. and western Canada (Sorensen 1983). Collections from Quebec and Ontario list the host as *Pinus banksiana*.

Discussion. —Because of previous misinterpretation of meso- and metanotal fusion in *Essigella* (see character discussion section), the description given here for this species is more accurate than that in Sorensen (1988).

Essigella (*E.*) *alyeska* is apparently uncommon; the limited collections of it preclude an adequate understanding of its morphological variation over its range. It is a broad-shaped species, but use of its body width characteristic, and that of the *E.* (*E.*) *knowltoni* complex, are not suggested for diagnostics because of the measurement error often associated with nonstandardized (compressed) slides that have been made by others. In contrast, I have attempted to standardize my *Essigella* slides for noncompression (Sorensen 1983) and, thus, have been able to use body width as an attribute in classification. This allowed the monophyletic
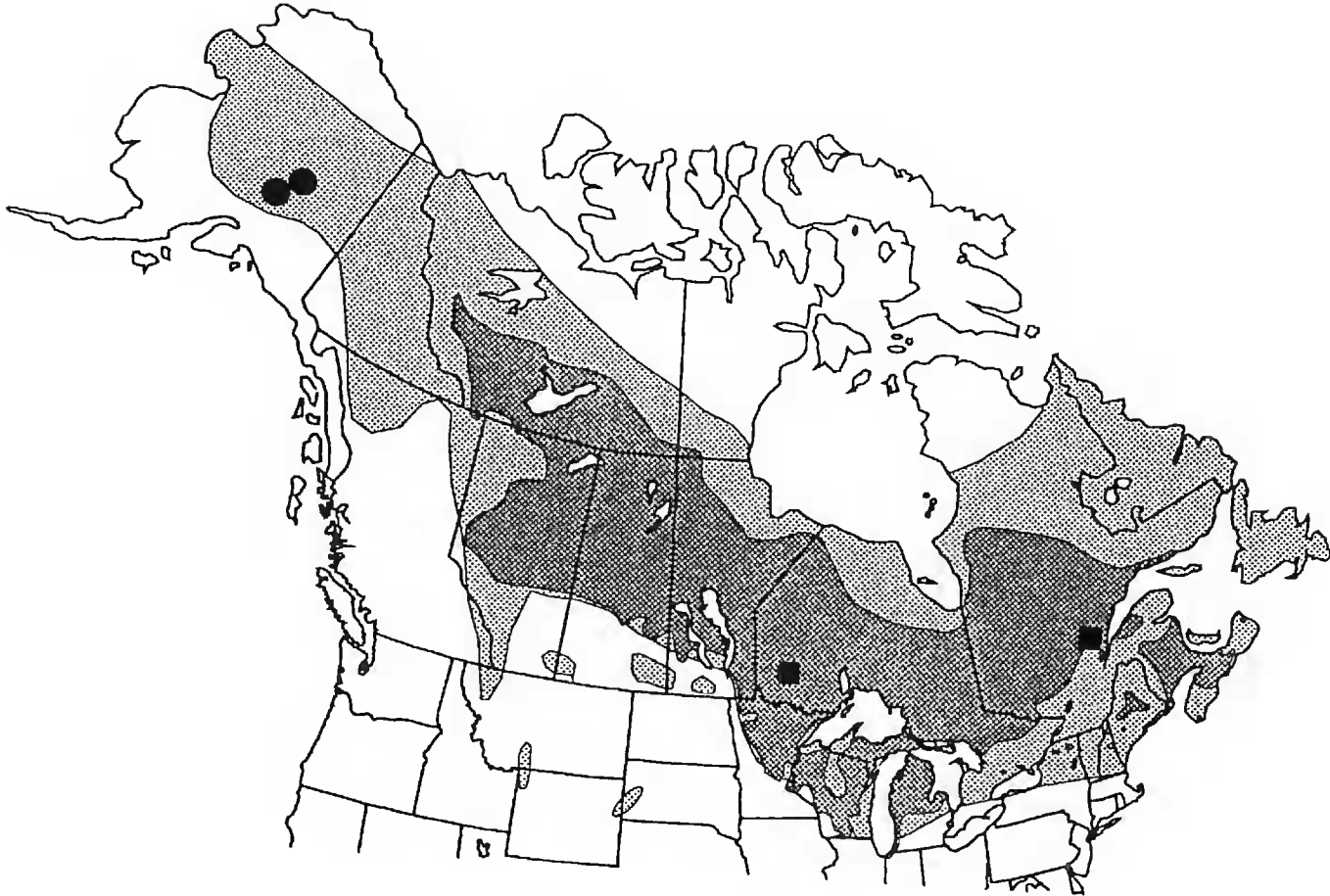
Figure 11. Distribution of *E*. (*E*.) *alyeska* [dots (JTS samples), squares (nonJTS samples)], super-imposed over the range of its hosts, *Picea glauca* [lighter shading (inclusive of darker)] and *Pinus banksiana* [darker shading].

grouping of *E*. (*E*.) *alyeska* with the *E*. (*E*.) *knowltoni* complex, on the basis of width as a nonhomoplasious synapomorphy. In the absence of use of that trait, several other homoplasies would have indicated a closer relationship to *E*. (*E*.) *wilsoni* (see discussion of that species). *Essigella* (*E*.) *alyeska* has no autapomorphies, or nonhomoplasious synapomorphies beyond its broad body width; most characters separating it from the *E*. (*E*.) *knowltoni* complex are reductions or losses.

Biology and biogeography also indicate its relationship to the *E*. (*E*.) *knowltoni* complex. The latter feed on the western members of *Pinus* (*Pinus*) Subsection Contortae, of which *P. banksiana* is an eastern member (Little & Critchfield 1969). *Essigella* (*E*.) *alyeska* superficially resembles very pale *E*. (*E*.) *critchfieldi,* despite several finer level differences. That resemblance, and *E*. (*E*.) *alyeska*'s central Alaskan distribution, which is very close to the potential Alaskan panhandle distribution of *E*. (*E*.) *critchfieldi* on *Pinus contorta contorta,* leads to the suspicion that these two species may be divergent sisters. That hypothesis is furthered by the proximity of these species on the phylogenetic tree derived from discriminant analysis (see the phylogenetics section). *Essigella* (*E*.) *alyeska* may have arisen from the progenitor of the *E*. (*E*.) *knowltoni* complex after the host capture of *Picea,* or when *P. contorta* and *P. banksiana* probably were separated during glaciations. In either event, these species, as members of the series B clade (Figs. 13–15), must have had an origin in the Arcto-Tertiary geoflora, unlike other *Essigella,* whose hosts had an origin in the Madro-Tertiary geoflora (Sorensen 1992a).

Coded References to This Taxon.—*Essigella* (*E*.) *alyeska* has been referred to previously by: the codings "Sp. D" (Sorensen 1983, 1987a, 1992b) and "ALYE" (Sorensen 1983), and by the manuscript name *E*. "*alyeska*" (Sorensen 1983).

Etymology and Common Name. — The aphid's species name is the Athabascan Indian term for "Alaska." Common name: the Alaskan conifer needle aphid.

Material Examined. — ALASKA. *FAIRBANKS NORTH STAR BOROUGH:* (type series) College, (Univ. Alaska Campus), nr Fairbanks, 24 Jun 1979, JTS 79F1, *Picea glauca,* (apt.). *BOROUGH UNCERTAIN:* 20 km NE of entrance Mt McKinley Natl Park, 15 Jul 1979, JTS 79G1, *Picea glauca,* (apt.). CANADA. *ONTARIO:* Perrault Falls, 17 Jul 1963, G. A. Bradley 63-147-O-APV, *Pinus banksiana. QUEBEC:* St. Bruno, Lac St. Jean, 10 Aug 1985, A. St. Hilaire, *Pinus banksiana.*

Essigella (Essigella) critchfieldi, NEW SPECIES

Essigella "critchfieldi" Sorensen, 1983: 112 (unpublished manuscript name) Ph.D. Thesis, University of California at Berkeley, Berkeley, California. 605 p.

Type Series. — Holotype, vivip. apt., on slide with 4 paratype vivip. apt., holotype in lower right (5 o'clock position); data: WASHINGTON. *GRAYS HARBOR Co.:* 16 km W of Amanda Park, hwy 101, 10 Jul 1978, J. T. Sorensen (78G56), *Pinus contorta contorta.* Holotype deposited in the Natural History Museum, London. Paratypes (all same data as holotype): 20 vivip. apt., on 5 slides including holotype slide. Paratype slides deposited: 1 slide in NMNH, Washington, D.C.; 1 slide in CNC, Ottawa, Ontario; 1 slide in Sorensen collection.

Viviparous Apterae. — *Morphology:* Body length: 1.65–1.88 (1.78 ± 0.08) mm. HEAD: Primary rhinarium on terminal antennal segment (V) not exceptionally distad, distance from tip of processus terminalis to distal face of rhinarial rim greater than $0.5 \times$ diameter of rhinarium; distal face of rhinarial rim usually oblique to longitudinal axis of antennal segment; rhinarial membrane not conspicuously protuberant. Length of antennal segment V: 100–163 (132 ± 16) μ, processus terminals: 30–43 (34 ± 4) μ; IV: 95–113 (102 ± 6) μ; III: 138–160 (147 ± 7) μ; II: 65–73 (70 ± 2) μ. Length of longest setae on frons: 28–55 (41 ± 7) μ, tips incrassate. Head width: 296–325 (308 ± 10) μ. Length of stylets: 510–653 (597 ± 41) μ; ultimate rostral segment: 65–78 (74 ± 4) μ, rostral tip reaching abdominal terga I–II, infrequently III, in dorsal view through slide-mounted specimens. Head + pronotum fused, total length: 326–418 (372 ± 39) μ. THORAX: Meso + metanota fused, total length: 316–357 (340 ± 17) μ. ABDOMEN: Tergum I free, length: 122–143 (132 ± 6) μ; terga II–VII fused, VIII free. Maximum distal width of flange on siphunculi: 39–50 (45 ± 4) μ; siphunculi protuberant, protrusion $0.5–0.8 \times$ maximal distal width. Ventral abdominal sclerites on segments III–IV subquadrate to subcircular; length: 38–48 (43 ± 3) μ, $1.0–1.4 \times$ diameter of metatibiae. Dorsal (major + minor) setae (see Fig. 1E) on abdominal terga III–IV: 8–9, tips sharp, in 1 row; marginal setae 3–4 each side, per segment. Setae on abdominal tergum VIII: usually 6, infrequently 7, anticipated rarely to 8, length: 23–40 (29 ± 5) μ, tips incrassate to sharp, in 1 row. Cauda broadly rounded; caudal protuberance moderately developed to absent; length of longest caudal setae: 50–100 (78 ± 15) μ, tips sharp. LEGS: Length of metafemora: 490–581 (529 ± 32) μ; metatibiae: 683–826 (760 ± 50) μ; longest dorsal setae on central one-third of metatibiae: 14–28 (22 ± 4) μ, $0.3–1.2 \times$ diameter of metatibiae, tips incrassate; approximately equal or very gradually increasing distally, no setal length dimorphism; longest ventral setae on metatibiae: 25–58 (39 ± 9) μ, tips sharp. Length of metabasitarsus: 98–110 (103 ± 3) μ; metadistitarsus: 153–178 (162 ± 8) μ. Ratio of metadistitarsus to metabasitarsus less than 1.9:1, mean 1.57:1. *Pigmentation:* Color in life: Black to very dark brown. Slide-mounted specimens: Background of body dorsum dark brown to nearly black (to nearly 100 percent pigment density), rarely pale, unicolorous. Terga at bases of setae on frons and dorsal (major + minor) setae on abdomen conclorous with surrounding terga; on dark individuals, dorsal (major + minor) setal sockets transparent, resembling pinholes. Thoracic muscle attachment plates and dorsal muscle attachment plates of abdomen moderate to dark brown, vaguely evident (dark individuals) to conspicuous (pale individuals). Spiracular plates and ventral abdominal sclerites moderate brown (light individuals) to nearly black (dark individuals). Siphunculi concolorous with surrounding terga. Cauda, anal and subgenital plates subtly to substantially darker than abdominal terga. Antennal segments V and IV concolorously dusky to moderate brown, paler than I and subtly paler than abdominal terga (dark individuals), rarely darker than I and abdominal terga (light individuals); III distal one-fifth to one-third dusky to moderate brown, remainder pale; II at least subtly darker than proximal III; I at least subtly darker than II and frons (all individuals) and substantially darker than V and IV (dark individuals). Pro-, meso- and

metatibiae all concolorous, as dark as (dark individuals) body tergum, to subtly darker (pale individuals). Distitarsi entirely moderately brown, to proximal tip sometimes subtly paler.

Ultimate Stadium Nymphs of Viviparous Apterae.—Slide-mounted specimens: Nonmorphometrics as described for viviparous apterae except lacking body dorsum pigmentation suite; abdominal terga membranous with dorsal (major + minor) setae, between muscle attachment plates, arising from distinct scleroites. Mesonotum with 2 sclerotized plates extending from muscle attachment sites to engulf neighboring setal bases; plates distinct, darkly pigmented, diameter approximately equaling eye length.

Viviparous Alatae, Oviparae, Males, Fundatrices.—Unknown.

Diagnosis.—*Essigella* (*E.*) *critchfieldi* is usually dark brown to nearly black, but infrequently nonteneral specimens are moderately brown. When dark, it is easily confused with *E.* (*E.*) *essigi* and *E.* (*E.*) *knowltoni knowltoni*. It lacks the abdominal tergum I fusion of *E.* (*E.*) *essigi*. It differs from *E.* (*E.*) *knowltoni knowltoni* by: having the darkest pigmentation of antennal segments IV and V at least subtly lighter, instead of subtly darker, than antennal segment I and the abdominal dorsum; usually having a wider maximal distal width of the siphunculi (more than, versus less, than 0.040 mm, although this is an indiscrete difference); and having the body dorsum unicolorous, rather than the frons and sometimes the head and anterad abdomen at least subtly lighter than the abdominal dorsum. The last character can be troublesome for separating *E.* (*E.*) *knowltoni knowltoni* from the Cascade range and southwestern regions of Oregon, where some individuals have the frons concolorously as dark as the abdomen. *Essigella* (*E.*) *critchfieldi* might also be confused with dark *E.* (*L.*) *eastopi* or aberrant, dark *E.* (*L.*) *fusca,* but differs from these by: having eight dorsal (major + minor) setae on abdominal terga III–IV in a single row (Fig. 1E), rather than double (or rarely single) row with the lateral-most minor dorsal seta in the anterad row (e.g., Fig. 1D); and having six, instead of eight, setae on abdominal tergum VIII. Additionally, the pigmentation patterns of *E.* (*L.*) *eastopi* and *E.* (*L.*) *fusca* differ [see their diagnoses].

Uncommon, pale *E.* (*E.*) *critchfieldi* individuals require the combination of several characters for identification. In particular, *E.* (*E.*) *alyeska* may be confused with these [see diagnosis: *E.* (*E.*) *alyeska*]. Pale *E.* (*E.*) *critchfieldi* can be diagnosed by their chaetotaxy pattern and the number of setae on abdominal terga III–IV and VIII (see above); by their ventral abdominal sclerites on abdominal segments III–IV always being large and subquadrate to subcircular; by the mesonotal muscle attachment plates on their later stadia nymphs of apterae being large and invasive; and by the longest dorsal setae on the central part of their mesotibiae being 0.5–1.5× tibial diameter, with tips always incrassate.

Range.—Coastal in: Washington, Oregon, northern California, and presumably British Columbia and the Alaskan panhandle (Fig. 12A).

Host.—*Pinus contorta contorta* Douglass ex Loudon; one collection (78G61) from *P. contorta latifolia* Englemann ex S. Watson shows *E.* (*E.*) *critchfieldi* and *E.* (*E.*) *knowltoni knowltoni* occur discretely in sympatry.

Discussion.—*Essigella* (*E.*) *critchfieldi* is the most divergent member of the *E.* (*E.*) *knowltoni* complex, and it was generally difficult to procure when sampling its host. It is relatively homogeneous in morphology, and is nearly always very dark when nonteneral. Its dark body dorsum is homoplasious within *E.* (*Essigella*), and causes confusion with evenly dark *E.* (*E.*) *knowltoni knowltoni* (e.g., Cascades) and the more distantly related *E.* (*E.*) *essigi*. The species' incrassate tips of the setae on the frons and dorsal setae on the metatibiae, regardless of their length,
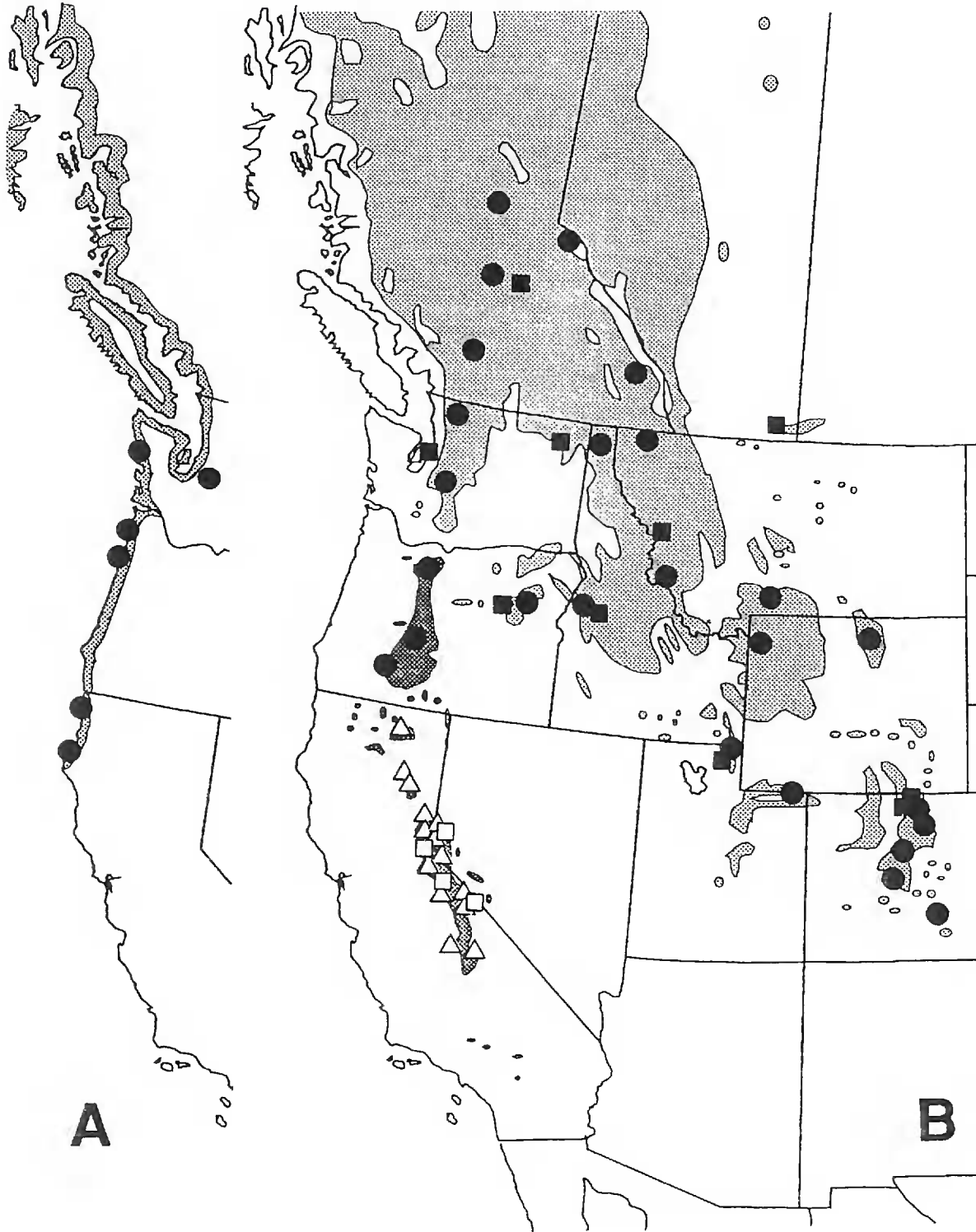
Figure 12.   Distribution of: A. *E.* (*E.*) *critchfieldi* [dots (JTS samples)], superimposed over the range of its host, *Pinus contorta contorta* [shaded]; B. *E.* (*E.*) *knowltoni knowltoni* [black dots (JTS samples), black squares (nonJTS samples)] and *E.* (*E.*) *knowltoni braggi* [white triangles (JTS samples), white squares (nonJTS samples)], superimposed over the range of their hosts, *Pinus contorta latifolia* [lighter shading] and *Pinus contorta murrayana* [darker shading (CA and cascade OR)].

is a synapomorphy for the *E.* (*E.*) *knowltoni* complex, as is its broad body. On *E.* (*E.*) *critchfieldi*, the length of dorsal setae on the central part of the metatibiae appears less variable and generally somewhat shorter than on *E.* (*E.*) *knowltoni*, but these setae are generally longer and more variable than on *E.* (*E.*) *essigi*. The lighter antennal pigmentation in *E.* (*E.*) *critchfieldi*, in contrast to the dark body dorsum, is an autapomorphy.

Sorensen (1992a) analyzed the relationships within the *E.* (*E.*) *knowltoni* complex, and in that study assigned populations of *E.* (*E.*) *critchfieldi* to the coastal group (Sorensen 1992a: COA). There [see discussion under *E.* (*E.*) *knowltoni knowltoni*], composite clusterings indicate that *E.* (*E.*) *critchfieldi* is the most divergent entity of the complex, and remained distinct until the ultimate clustering

level. Its relative distinction was confirmed by principal component and discriminant function analyses, both of which indicate that it is less like either of the *E. (E.) knowltoni* subspecies than they are to themselves. The analyses showed that *E. (E.) critchfieldi* separates from the most geographically proximal populations of *E. (E.) knowltoni* [the equally and evenly dark, Cascade *E. (E.) knowltoni knowltoni*] by the relative difference, albeit subtle, in pigmentation of its antennal segments, the distal width of its extended siphuncular flange, and its smaller general size. It separates easily from *E. (E.) knowltoni braggi* because the latter has much paler general pigmentation. Character displacement involving qualitative and qualitative traits occurs within this aphid complex [see discussion of *E. (E.) knowltoni*].

Coded References to This Taxon. — *Essigella (E.) critchfieldi* has been referred to previously by the codings: "Sp. E" (Sorensen 1983, 1987a, 1992b), "CRIT" (Sorensen 1983), and "COA" (Sorensen 1992a). Sorensen (1983) referred to this taxon under the manuscript name *E. "critchfieldi."*

Etymology and Common Name. — The species is named for the botanist and plant geneticist W. B. Critchfield, who provided much of the information on pines and their relatedness that was necessary for this aphid revision. Common name: Critchfield's shore pine needle aphid.

Material Examined. — CALIFORNIA. *DEL NORTE Co.:* Crescent City, 4 Jul 1978, JTS 78G5, *P. c. contorta,* (apt.). *HUMBOLT Co.:* Manila, 7 km W of Arcata on hwy 255, 3 Jul 1978, JTS 78G2, *P. c. contorta,* (apt.). OREGON. *CLATSOP Co.:* Seaside, 7 Jul 1978, JTS 78G46, *P. c. contorta,* (apt.). *TILAMOOK Co.:* Pacific City, 7 Jul 1978, JTS 78G44, *P. c. contorta,* (apt.). WASHINGTON. *GRAYS HARBOR Co.:* (type series) 16 km W of Amanda Park on hwy 101, 10 Jul 1978, JTS 78G56, *P. c. contorta,* (apt.). *YAKIMA Co.:* E side of Chinook Pass on hwy 410, 1310 m, 11 Jul 1978, JTS 78G61, *P. c. latifolia,* (apt.).

Essigella (Essigella) knowltoni knowltoni Hottes, 1957, NEW STATUS

Essigella knowltoni Hottes, 1957: 92, Proc. Biol. Soc. Wash., 70: 92–93.

Primary Type. — Lectotype, vivip. apt., on slide with 3 other apt., lectotype in lower right corner; slide data: "Colo. Aphids, Host *Pinus contorta* var. *muriana, Essigella fusca* G. & P., Pink-gree Park, Color., Date 23 Aug 1935, G. F. Knowlton-collector/Holotype *Essigella knowltoni* F. C. Hottes (over)/[on back] *Essigella knowltoni knowltoni* Hottes, lectotype, designated J. T. Sorensen, 1981/[specimen position map on slide label] Lectotype Sorensen 1981, as seen from this side." Lectotype deposited in the U.S. National Museum of Natural History, Washington, D.C.

There is confusion concerning the type designation. Hottes (1957: 93) designated a holotype (data as above). The slide has "holotype" written on it, and a circle drawn to indicate the individual, but there is no specimen subtending, or even near, the designation circle. I have selected one of the same morph on the slide as technical lectotype, because no single individual was identifiable as the "holotype."

Viviparous Apterae. — *Morphology:* Body length: 1.60–2.32 (1.99 ± 0.21) mm. HEAD: Primary rhinarium on terminal antennal segment (V) not exceptionally distad, distance from tip of processus terminalis to distal face of rhinarial rim greater than 0.5× diameter of rhinarium; distal face of rhinarial rim usually oblique to longitudinal axis of antennal segment; rhinarial membrane not conspicuously

protuberant. Length of antennal segment V: 108–150 (132 ± 12) μ, processus terminalis: 28–50 (39 ± 5) μ; IV: 78–115 (100 ± 9) μ; III: 148–218 (184 ± 20) μ; II: 63–95 (75 ± 6) μ. Length of longest setae on frons: 20–73 (44 ± 14) μ, tips incrassate. Head width: 296–377 (333 ± 23) μ. Length of stylets: 520–836 (658 ± 74) μ; ultimate rostral segment: 69–90 (80 ± 5) μ, rostral tip reaching abdominal terga I–III in dorsal view through slide-mounted specimens. Head + pronotum fused, total length: 367–479 (420 ± 33) μ. THORAX: Meso + metanota fused, total length: 306–449 (373 ± 42) μ. ABDOMEN: Tergum I free, length: 102–173 (142 ± 18) μ; terga II–VII fused, VIII free. Maximum distal width of flange on siphunculi: 28–44 (36 ± 3) μ; siphunculi nearly flush to truncated conical, protruding to 0.6× maximum distal width. Ventral abdominal sclerites on segments III–IV subcircular to less commonly subelliptical, length: 40–68 (54 ± 7) μ, 1.0–1.6× diameter of metatibiae. Dorsal (major + minor) setae (see Fig. 1E) on abdominal terga III–IV: 8–10, tips sharp, in 1 row, often irregular with setae next to most mesad slightly anterad, or most mesad pair slightly posterad; marginal setae 3–4 each side. Setae on abdominal tergum VIII: 6, infrequently 7, very rarely to 8 (anticipated), length: 20–63 (39 ± 12) μ, tips incrassate to sharp, in 1 row. Cauda broadly rounded; caudal protuberance usually absent to poorly developed, sometimes to moderately developed; length of longest caudal setae: 70–123 (96 ± 16) μ, tips sharp. LEGS: Length of metafemora: 479–775 (655 ± 77) μ; metatibiae: 669–1102 (939 ± 127) μ; longest dorsal setae on central one-third of metatibiae: 10–78 (39 ± 18) μ, 0.3–2.3× diameter of metatibiae, tips incrassate; approximately equal or very gradually increasing distally, no setal length dimorphism; longest ventral setae on metatibiae: 25–50 (38 ± 8) μ, tips sharp. Length of metabasitarsus: 105–163 (131 ± 14) μ; metadistitarsus: 150–230 (195 ± 18) μ. Ratio of metadistitarsus to metabasitarsus less than 1.9:1, mean 1.49:1. *Pigmentation:* Color in life: Body usually dark brown to black, infrequently gray-green or gray; when dark, frons usually paler, yellow. Slide-mounted specimens: Background of body dorsum variable, usually moderately brown to often nearly black (to nearly 100 percent pigment density), occasionally moderately pale to light brown; when dark, frons and sometimes anterad of thorax usually paler than abdominal dorsum; dorsum rarely slightly mottled, or abdominal dorsum rarely darkened more dorsomedially. Terga at bases of setae on frons and dorsal (major + minor) setae on abdomen concolorous with surrounding terga; on dark individuals, dorsal (major + minor) setal sockets transparent, resembling pinholes; occasionally on paler specimens pigmentation of setal bases on abdominal terga subtly darkened and laterally expanded to form a nearly complete, vague band on each terga. Thoracic muscle attachment plates and dorsal muscle attachment plates of abdomen conspicuous, slightly darker than (pale individuals) to as dark as (dark individuals) abdominal terga. Spiracular plates and ventral abdominal sclerites conspicuous, usually dark brown to nearly black (dark individuals), rarely pale (pale individuals). Siphunculi concolorous with surrounding terga. Cauda, anal and subgenital plates slightly darker than (pale individuals) to as dark as (dark individuals) abdominal terga. Antennal segments V and IV moderate to very dark brown, often distal one-half paler, infrequently pale individuals with proximal one-third of IV paler; III usually moderate to dark brown on distal one-half, remainder pale, infrequently entirely pale (pale individuals), rarely proximal one-half moderate brown and substantially darker distally (dark individuals); II concolorous with proximal III; I concolorous with frons, always lighter than darkest part of V and IV. Pro-, meso- and metatibiae concolorous but variable, usually equivalent with (dark individuals) abdominal terga, often paler, infrequently slightly darker (pale individuals); infrequently tibiae dusky at both tips, paler centrally. Distitarsi variable with tibiae, entirely dark to dusky on distal one-third, proximally paler.

Ultimate Stadium Nymphs of Viviparous Apterae.—Slide-mounted specimens: Nonmorphometrics as described for viviparous apterae except lacking body dorsum pigmentation suite; abdominal terga membranous with dorsal (major + minor) setae, between muscle attachment plates, arising from distinct scleroites. Mesonotum with 2 sclerotized plates extending from muscle attachment sites to engulf neighboring setal bases; plates usually distinct, faintly to heavily pigmented, diameter approximately equaling eye length.

Viviparous Alatae.—Slide-mounted specimens: Nonmorphometrics as described for viviparous apterae except lacking body dorsum pigmentation suite; abdominal terga normally membranous, dorsal (major + minor) setae between muscle attachment plates frequently arising from distinct scleroites; antennal segments often as dark as tibiae, except proximal one-fifth of III pale. Antennal segment III with 0–5, IV with 0, secondary rhinaria. Epicranial suture usually absent, to vaguely developed. Forewing medius with single furcation, very rarely 2 or rarely medius single, (if 2, then first) furcation point usually arising on proximad, infrequently on central or distad, one-third of vein; cubital base usually arising distad, infrequently proximad, on subcosta with distance between anal and cubital bases on subcosta usually relatively large, ca. 30–40 percent or more of anal vein length; medius,

especially cubitus and anal veins distinct, except infrequently proximad 10–15 percent vague. Abdominal terga frequently with irregular sclerites that engulf or join muscle attachment plates and dorsal (major + minor) setal bases or scleroites.

Oviparae.—Slide-mounted specimens: Nonmorphometrics as described for viviparious apterae, abdominal terga II–VII fused, moderately to heavily sclerotic, including pleural areas, tergum VIII free; dorsal demarcations of anterad terga not evident; siphunculi incorporated into sclerotic dorsum; dorsal abdominal muscle attachment plates unicolorous. Pseudorhinaria on metatibiae irregular, 8–9.

Males, Fundatrices.—Unknown.

Diagnosis.—*Essigella* (*E.*) *knowltoni* can be difficult to distinguish because it varies in body pigmentation from pale to nearly black. These are relatively wide (broad) aphids, for *Essigella,* but that trait is shared with *E.* (*E.*) *critchfieldi* and *E.* (*E.*) *alyeska,* and is very easily distorted by slide compression [see discussion of *E.* (*E.*) *alyeska*]; therefore, it is not recommended. Although dark individuals can be confused with *E.* (*E.*) *essigi* and *E.* (*E.*) *critchfieldi, E.* (*E.*) *knowltoni* lacks the abdominal tergum I fusion of *E.* (*E.*) *essigi,* and differs, most reliably, from *E.* (*E.*) *critchfieldi* in having antennal segments IV and V at least subtly darker, rather than lighter, than antennal segment I. *Essigella* (*E.*) *knowltoni* also may be confused with dark *E.* (*L.*) *eastopi* or dark, aberrant *E.* (*L.*) *fusca,* but differs from these as *E.* (*E.*) *critchfieldi* does [see diagnosis: *E.* (*E.*) *critchfieldi*]. Pale *E.* (*E.*) *knowltoni* individuals can be confused with most pale *Essigella,* and require the combination of several characters for identification. They differ from (my limited samples of) *E.* (*E.*) *alyeska* by having three to four, rather than two, marginal setae on abdominal terga III–IV, and always large and invasive, rather than small and noninvasive, muscle attachment plates on the mesonotum of later stadia nymphs of apterae. They differ from *E.* (*E.*) *californica, E.* (*E.*) *hoerneri* and *E.* (*E.*) *pini* by having eight to infrequently 10 (Fig. 1E), rather than six, dorsal (major + minor) setae on abdominal terga III–IV. They lack the protuberant, exceptionally distad primary rhinarium of *E.* (*E.*) *wilsoni,* and the exceptionally long metadistitarus and short metabasitarsus of *E.* (*A.*) *kathleenae.* Many pale *E.* (*L.*) *eastopi, E.* (*L.*) *fusca* and *E.* (*L.*) *hillerislambersi* may be confused with pale *E.* (*E.*) *knowltoni*; individuals with sharp dorsal setae on the metatibiae can be distinguished from *E.* (*E.*) *knowltoni,* which always have these setae incrassate, regardless of length; other *E.* (*E.*) *knowltoni* with fewer than eight setae on abdominal tergum VIII can be separated from these three species, which always have eight or more such setae. Problems arise in separating pale *E.* (*E.*) *knowltoni* with eight or more setae on abdominal tergum VIII from pale *E.* (*L.*) *eastopi, E.* (*L.*) *fusca* and *E.* (*L.*) *hillerislambersi* with incrassate or blunt dorsal setae on the metatibiae; such *E.* (*L.*) *fusca, E.* (*L.*) *hillerislambersi* and (usually) *E.* (*L.*) *eastopi* have dorsal (major + minor) setae on abdominal terga III–IV in two rows with the lateral-most minor dorsal seta in the anterad row (e.g., Fig. 1C); although rare *E.* (*E.*) *knowltoni braggi* may approach this condition, they usually resemble Fig. 1D. In *E.* (*L.*) *fusca* and *E.* (*L.*) *hillerislambersi,* the ventral abdominal sclerites on segments III–IV vary from small to large and sublinear, but not large and subcircular-subelliptical, as is always the case for *E.* (*E.*) *knowltoni.* Odd, pale *E.* (*E.*) *knowltoni* [usually *E.* (*E.*) *k. braggi*] with 10 setae on abdominal tergum VIII, and short dorsal setae on the metatibiae, might be potentially confused with *E.* (*A.*) *kirki* [see diagnosis: *E.* (*A.*) *kirki*].

Separation of the *E.* (*E.*) *knowltoni* subspecies depends chiefly on pigmentation differences, because univariate traits overlap to a large degree. However, pig-

mentation differences between *E. (E.) knowltoni knowltoni* and *E. (E.) knowltoni braggi* can be subtle for paler specimens. *Essigella (E.) k. knowltoni* are usually dark, ranging to nearly black, and usually have the frons, and sometimes the entire head and anterad of the thorax, paler than the abdominal terga; some specimens from the Cascade Range and southwest Oregon have the frons as dark (to black) as the rest of the body dorsum. Most *E. (E.) k. braggi* are pale, rarely moderately dark, but then always with the frons concolorous with the body dorsum; they have six to often eight, rarely 10, setae on abdominal tergum VIII, versus the six, to rarely eight for *E. (E.) k. knowltoni*. The degree of sclerotization of the terga, and the subgenital and anal plates, for *E. (E.) k. braggi* is less than for equivalently pigmented *E. (E.) k. knowltoni. Essigella (E.) k. braggi* individuals have indiscretely longer metatibiae for their body length, than do *E. (E.) k. knowltoni*. See couplet 16 in the key to the viviparous apterae for separation of these subspecies.

Range. — Interiors of Oregon, Washington and British Columbia; south through the Rocky Mountains to central Utah and southern Colorado (Fig. 12B). [For species, see *E. (E.) knowltoni braggi* also.]

Hosts. — *Pinus contorta latifolia* Engelmann ex S. Watson; *P. contorta murrayana* Greville & Balfour (only to southern Oregon). [For species, see *E. (E.) knowltoni braggi* also.].

Discussion. — This species [including *E. (E.) k. braggi* as a subspecies], and *E. (E.) critchfieldi,* comprise the *E. (E.) knowltoni* complex. A unique, qualitative synapomorphy for this complex is that the tips of the setae on the frons and dorsum of the central part of the metatibiae are always incrassate, regardless of the length of those setae. The complex also has a broad body, which is a synapomorphy with *E. (E.) alyeska,* denoting a clade on subsection Contortae pines within *E. (Essigella)* [see discussion of *E. (E.) alyeska*]. The fusion of the abdominal terga of the oviparae for *E. (E.) knowltoni* is problematic [see the character discussion section].

Essigella (E.) knowltoni shares the *Pinus contorta* niche with *E. (E.) critchfieldi,* but occurs only on the interior (noncoastal) morphocline of *P. contorta latifolia-murrayana.* Sorensen (1992a) analyzed and discusses the taxonomic and host relationships within the complex, as coded groups of populations. In those analyses, *E. (E.) k. knowltoni* and *E. (E.) k. braggi* represent the populations assigned to the Cascade-Rocky Mountain (Sorensen 1992a: CAS + RMT) and the Sierra Nevada (Sorensen 1992a: SNV) groups, respectively. The analyses, using exemplars from populations, combined character information from both coded qualitative traits and factor loading scores derived from principal component analyses. The composite data was then clustered, and showed that the groupings of populations that make up *E. (E.) k. knowltoni* and *E. (E.) k. braggi* are best circumscribed separately. These groups of populations show somewhat divergent trends in their covariance distributions of morphometric traits in the attribute space defined by principal component analysis, but both differ markedly from the populations comprising *E. (E.) critchfieldi* (Sorensen 1992a: fig. 5). The closer relationship of the *E. (E.) knowltoni* subspecies to one another, in comparison with either to *E. (E.) critchfieldi,* was also confirmed by discriminant function analysis (Sorensen 1992a: fig. 6).

The subspecies of *E. (E.) knowltoni* break in the Klamath-Siskiyou region (California-Oregon border) along the *Pinus contorta latifolia-murrayana* mor-

phocline, which arcs around the Great Basin and Columbia Plateau. Interestingly, this schism of aphid populations does not occur slightly further north, at the Columbia river (Oregon-Washington border), where Critchfield (1957) states the morphological break in the *P. c. latifolia-murrayana* morphocline, itself, occurs. The Klamath-Siskiyou area marks a steep terpene gradient within *Pinus contorta murrayana*, which separates the California Sierra Nevada populations of the tree from those of the Cascades (Forrest 1980). Thus, the aphid relationships within the *E. (E.) knowltoni* complex show excellent geographic congruence with the genic and biochemical diversity in the *Pinus contorta* complex (Wheeler & Guries 1982a, b; Wheeler et al. 1983).

Essigella (E.) k. knowltoni is the most variable of the two subspecies, grading from completely pale to nearly black within populations; Sorensen (1992a: figs. 2a–d) shows maps depicting qualitative character variance over geography. Rocky Mountain populations have the highest incidence of pale individuals, show the greatest size variation, and generally have the longest (but quite variable) dorsal setae on the metatibiae. Populations from British Columbia are similar to those of the Rocky Mountains, except darker individuals show greater development of the paleness of the frons and usually the entire head and anterad of the thorax. Dark individuals from Oregon cascade populations often show the frons to be unicolorously as dark as the rest of the body dorsum, as does *E. (E.) critchfieldi*. Populations of *E. (E.) k. braggi* are pale to seldom moderately brown, but then always have the entire body dorsum unicolorous.

Pigmentation suites within the *E. (E.) knowltoni* complex do not appear influenced by host or environment. For example, a collection of specimens (77G61) of *E. (E.) k. braggi* spuriously from *Pinus monticola* maintained their characteristic pigmentation suite, despite occurring opportunistically on that haploxylon pine. Analysis of 25 environmental variables (unpublished data) from sample locations, in relation to qualitative characteristics of individuals from those samples, did not appear to indicate relatedness.

Within the *E. (E.) knowltoni* complex, the pigmentation suite is involved in a character displacement phenomenon (Sorensen 1992a) that also involves general-size. Among the most geographically proximal populations of *E. (E.) knowltoni knowltoni, E. (E.) knowltoni braggi* and *E. (E.) critchfieldi*, where these taxa are relatively adjacent in southern Oregon and northern California, those sharing the most similar pigmentation differ the most markedly in covariance relationships among morphometric traits and general-size, and vice versa. When the adjacent populations of these taxa are similarly colored, they differ in size, but when similar in size, they differ in color. The body is relatively unicolorously dark or pale in these geographic areas, but becomes differentiated, as gradiently bicolored, in *E. (E.) knowltoni knowltoni* in the Rocky Mountains, at a maximal distance from the zone of contact (Sorensen 1992a: figs. 2a–c).

Although I consider the populations that comprise *E. (E.) k. knowltoni* and *E. (E.) k. braggi* to be subspecific, based upon the relative anagenic distance between them when compared to *E. (E.) critchfieldi* (Fig. 13; Sorensen 1992a: fig. 6), they are definitely more distinct (nonclinal) than the subspecies of *E. (L.) fusca*. The subspecific status of *E. (E.) k. braggi* is assigned here to reflect the relative inter-taxon distances shown by Sorensen (1992a); however, it would be more appropriate to elevate *E. (E.) k. braggi* to full species status, rather than synonymize

it. Hottes (1957) apparently did not recognize the relationship between his *E. "knowltoni"* and *E. "braggi"* [or *E. "robusta"*], which he believed to be separate species; although he does contrast his *E. "braggi"* with *E. "robusta,"* suggesting an awareness of similarity between them. He considered his *E. "knowltoni"* [here *E. (E.) knowltoni knowltoni*] to be "perhaps most closely allied to *E. essigi,"* citing the dorsal darkness of the body. Toward the beginning of this study, Dirk Hille Ris Lambers (personal communication [1980]), also citing the dark body dorsum, but without close examination, indicated that he thought my collections of *E. (E.) knowltoni knowltoni, E. (E.) critchfieldi* and *E. (E.) essigi* were conspecific, whereas *E. (E.) knowltoni braggi* was distinct. Several analyses (Sorensen 1983, 1987a, 1992a, b, unpublished data) indicate that the melanic dorsum trait, which varies to pale within many of the populations of all those species that display it, is homoplasious within *E. (Essigella).*

Coded References to This Taxon.—*Essigella (E.) knowltoni knowltoni* has been referred to previously by the codings: "Sp. F" (Sorensen 1983, 1987a, 1992b), "KNOW" (Sorensen 1983), and "CAS + RMT" (Sorensen 1992a). Sorensen (1983) referred to this taxon under the name *E. knowltoni knowltoni.*

Etymology and Common Name.—This species was named for G. F. Knowlton, who collected the holotype (Hottes 1957: 93), and had a long time friendship with F. C. Hottes that began when they were students under A. A. Granovsky (G. F. Knowlton, personal communication). Common name: Knowlton's lodgepole pine needle aphid.

Material Examined.—[*E. (E.) knowltoni knowltoni* only:] COLORADO. *CLEAR CREEK Co.:* Empire, 2530 m, 14 Aug 1978, JTS 78H86, *P. ponderosa,* (apt.). *GRAND Co.:* 24 km NW of Grandby on hwy 125, 2530 m, 15 Aug 1978, JTS 78H90, *P. c. latifolia,* (apt., ovip.). *GUNNISON Co.:* W side of Monarch Pass on hwy 50, 2870 m, 13 Aug 1978, JTS 78H74, *P. c. latifolia,* (apt.). *HUERFANO Co.:* North La Veta Pass Summit on hwy 160, 2870 m, 12 Aug 1978, JTS 78H63, *P. c. latifolia,* (apt.). *LAKE Co.:* 11 km W of Twin Lakes on hwy 82, 3050 m, 14 Aug 1978, JTS 78H77, *P. c. latifolia,* (apt., ovip.). *LARIMER Co.:* (paratype) Cameron Pass, 18 Aug 1940, G. F. Knowlton, *P. c. latifolia,* (apt.); (lectotype) Pingree Park, 23 Aug 1935, G. F. Knowlton, *P. contorta* var. *"muriana,"* (apt.); (paratype) same but 19 Aug 1935, *P. c. latifolia,* (apt.). IDAHO. *ADAMS Co.:* Tamarack, 18 Jul 1978, JTS 78G110, *P. c. latifolia,* (apt.). *BONNER Co.:* 6 km S of Cocolalla on hwy 95, 18 Jul 1978, JTS 78G104, *P. c. latifolia,* (apt.). *VALLEY Co.:* McCall, 5 Jun 1978, C. S. Smith, CFS 78-170, *P. c. latifolia,* (apt.). MONTANA. *FLATHEAD Co.:* 16 km S of Stryker on hwy 93, 17 Jul 1978, JTS 78G97, *P. c. latifolia,* (apt.). *PARK Co.:* Silver Gate, hwy 212, 2170 m, 21 Aug 1978, JTS 78H122, *P. c. latifolia,* (apt.). *RAVALLI Co.:* Chief Joseph Pass on hwy 13 [93?] on continental divide, 17 Jul 1979, D. J. Voegtlin, DJV 692, *P. c. latifolia,* (apt.). OREGON. *BAKER Co.:* Blue Mt Summit on hwy 26, 20 Jul 1978, JTS 78G113, *P. c. latifolia,* (apt.). *GRANT Co.:* Canyon Meadows Cmpgd, Malheur Natl Forest, nr John Day, 21 Aug 1979, D. J. Voegtlin, DJV 613, *P. c. murrayana,* (apt.). *JACKSON Co.:* 3 km E of Union Creek on hwy 62, 1100 m, 5 Jul 1978, JTS 78G19, *P. c. murrayana,* (apt.). *KLAMATH Co.:* 16 km S of LaPine on hwy 97, 5 Jul 1978, JTS 78G22, *P. c. murrayana,* (apt., alat.). *WASCO Co.:* 46 km SE of Government Camp on hwy 26, 670 m, 6 Jul 1978, JTS 78G32, *P. c. murrayana,* (apt.). UTAH. *CACHE Co.:* 11 km W of Garden City on hwy 89, 2350 m, 24 Aug 1978, JTS 78H133, *P. c. latifolia,* (apt.); Beaver Creek, Logan Cyn, 25 Jul 1929 Aug 1937, C. F. & C. S. Smith, *P. c. latifolia,* (apt.). *DAGGETT Co.:* 32 km S of Manila on hwy 44, 2400 m, 24 Aug 1978, JTS 78H139, *P. c. latifolia,* (apt.). WASHINGTON. *FERRY Co.:* Sherman Pass, Colville Natl Forest, 14 Sep 1979, D. J. Voegtlin, DJV 751, *P. c. latifolia,* (alat.). *KING Co.:* Arboretum, Seattle, 12 Aug 1956, M. J. Forsell, *P. contorta,* (apt.). *WHATCOM Co.:* NE of Newhalem on hwy 20, 300 m, 12 Jul 1978, JTS 78G76, *P. c. latifolia,* (apt.). *YAKIMA Co.:* E side of Chinook Pass on hwy 410, 1310 m, 11 Jul 1978, JTS 78G61, *P. c. latifolia,* (apt.). WYOMING. *JOHNSON Co.:* 26 km W of Buffalo on hwy 16, 2290 m, 19 Aug 1978, JTS 78H105, *P. c. latifolia,* (apt.). *TETON Co.:* Huckleberry Hotsprings, hwy 287, between Yellowstone & Grand Teton Natl Parks, 2010 m, 23 Aug 1978, JTS

78H124, *P. c. latifolia*, (apt., alat., ovip.). CANADA. *ALBERTA:* 3 km (2 mi) S of Cypress Hills, 18 Jul 1966, P. Rauch, RVdB CL66-VII-18B, *P. c. latifolia*, (apt.). BRITISH COLUMBIA. 21 km S of 100 Mile House on hwy 97, 910 m, 13 Jul 1978, JTS 78G82, *P. c. latifolia*, (apt.); 40 km E of Prince George on hwy 16, 14 Jul 1978, JTS 78G85, *P. c. latifolia*, (apt.); 5 km N of Spuzzum on hwy 1, 13 Jul 1978, JTS 78G77, *P. monticola*, (apt.); 7 km S of Canal Flats on hwy 93, 17 Jul 1978, JTS 78G95, *P. c. latifolia*, (apt.); Mt Robson Prov Park, 15 Jul 1978, JTS 78G88, *P. c. latifolia*, (apt.); nr Clearwater, 9 Sep 1979, D. J. Voegtlin, DJV 744, *P. c. latifolia*, (apt.).

Essigella (*Essigella*) *knowltoni braggi* Hottes, 1957, NEW STATUS

Essigella braggi Hottes, 1957: 73, Proc. Biol. Soc. Wash., 70: 73–75.
Essigella robusta Hottes, 1957: 103, Proc. Biol. Soc. Wash., 70: 103–105. NEW SYNONYM.

Primary Type. —Holotype, vivip. apt., on slide with 4 other apt., holotype shown by arrow (upper right); slide data: "*Pinus contorta,* Tuolumne Meadows, Calif., VIII-22-1955, J. W. MacSwain/Holotype, *Essigella braggi* F. C. Hottes" (Tuolumne Meadows is in Tuolumne Co., in Yosemite National Park, west of Tioga Pass). Holotype deposited in the Essig Museum of Entomology, University of California at Berkeley, Berkeley, California.

Viviparous Apterae.—Morphology: As *E.* (*E.*) *knowltoni knowltoni,* except as follows. Body length: 1.67–2.39 (2.04 ± 0.21) mm. HEAD: Length of antennal segment V: 125–153 (141 ± 9) μ, processus terminalis: 33–63 (41 ± 8) μ; IV: 95–118 (107 ± 7) μ; III: 168–215 (190 ± 17) μ; II: 70–88 (77 ± 4) μ. Length of longest setae on frons: 28–78 (52 ± 12) μ. Head width: 316–398 (349 ± 22) μ. Length of stylets: 632–816 (718 ± 60) μ; ultimate rostral segment: 68–88 (81 ± 6) μ, rostral tip reaching abdominal terga I–II in dorsal view through slide-mounted specimens. Total length of fused head + pronotum: 393–490 (438 ± 29) μ. THORAX: Total length of fused meso + metanota: 296–439 (381 ± 39) μ. ABDOMEN: Tergum I length: 112–173 (149 ± 20) μ. Maximum distal width of flange on siphunculi: 25–45 (37 ± 6) μ. Ventral abdominal sclerite length: 48–65 (56 ± 6) μ. Dorsal (major + minor) setae (see Fig. 1E) on abdominal terga III–IV: 8–10, rarely to 12, when 12 the lateral-most minor dorsal seta usually anterad of its next mesad neighbor (i.e., Fig. 1D). Setae on abdominal tergum VIII: 6–8, rarely to 10, length: 23–88 (52 ± 16) μ, in 1 row, to 2 when 12. Length of longest caudal setae: 70–125 (93 ± 15) μ. LEGS: Length of metafemora: 622–842 (724 ± 61) μ; metatibiae: 928–1219 (1048 ± 76) μ; longest dorsal setae on central one-third of metatibiae: 25–55 (39 ± 9) μ; longest ventral setae on metatibiae: 23–48 (34 ± 7) μ. Length of metabasitarsus: 125–158 (140 ± 11) μ; metadistitarsus: 190–225 (206 ± 12) μ. Mean ratio of metadistitarsus to metabasitarus: 1.47:1. *Pigmentation:* As *E.* (*E.*) *knowltoni knowltoni,* except as follows. Color in life: Gray-green or gray to light brown, throughout. Slide-mounted specimens: Background of body dorsum pale to light brown (to 40 percent pigment density), unicolorous. Terga at bases of setae on frons and dorsal (major + minor) setae on abdomen concolorous with surrounding terga, infrequently subtly darker. Thoracic muscle attachment plates and dorsal muscle attachment plates of abdomen usually substantially darker than body dorsum, often only subtly darker. Spiracular plates and ventral abdominal sclerites conspicuous, usually dark brown, infrequently light brown, but always darker than body dorsum. Cauda, anal and subgenital plates usually substantially darker than abdominal terga, often only slightly darker. Antennal segments with darkest areas usually moderate brown, sometimes lighter; proximal base of III never moderate brown; II usually concolorous with proximal one-half of III, but infrequently darker. Pro-, meso- and metatibiae usually pale to frequently moderately brown, often substantially darker than abdominal dorsum.

Diagnosis. —For separation of the *E.* (*E.*) *knowltoni* subspecies, see the diagnosis of *E.* (*E.*) *knowltoni knowltoni,* and couplet 16 in the key to the viviparous apterae.

Synonyms.—Essigella robusta Hottes, NEW SYNONYM: lectotype (formerly "holotype"), vivip. apt., on slide with 7 other specimens (lectotype in 10 o'clock position); data: CALIFORNIA. *EL DORADO Co.:* Upper Echo Lake, 2285 m

(7500 ft), 6 Aug 1937, E.O.E[ssig]., *Pinus contorta murrayana. Essigella robusta* lectotype deposited in the Essig Museum of Entomology, University of California at Berkeley, Berkeley, California. Although Hottes (1957: 104–105) designated a "holotype" for *E. robusta,* his designation circle on the slide encompasses 2 adult and 1 nymphal vivip. apt.; I have selected the center specimen within the designation circle as technical lectotype, because no single individual was clearly identifiable as "holotype."

Range. —Sierra Nevada and Cascades of California (Fig. 12B). [For species, see *E.* (*E.*) *knowltoni knowltoni* also.]

Host. —*Pinus contorta murrayana* Greville & Balfour (south of the Oregon-California border only) (see discussion). [For species, see *E.* (*E.*) *knowltoni knowltoni* also.]

Discussion. —See *E.* (*E.*) *knowltoni knowltoni.*

Coded References to This Taxon. —*Essigella* (*E.*) *knowltoni braggi* has been referred to previously by the codings: "Sp. G" (Sorensen 1983, 1987a, 1992b), "BRAG" (Sorensen 1983), and "SNV" (Sorensen 1992a). Sorensen (1983) referred to this taxon under the manuscript name *E.* "*knowltoni braggi.*"

Etymology and Common Name. —Hottes (1957:) named "*Essigella braggi*" for L. C. Bragg, presumably because he collected many aphids early in this century; I cannot find reference, however, to his association with "*Essigella braggi*" in particular. Common name: Bragg's lodgepole pine needle aphid.

Material Examined. —[*E.* (*E.*) *knowltoni braggi* only:] CALIFORNIA. *ALPINE Co.:* E side of Ebbett's Pass on hwy 4, 3 km E of summit, 2400 m, 17 Jul 1977, JTS 77G42, *P. c. murrayana,* (apt.); same but JTS 77G41, *P. monticola,* (apt.); Upper Cascade Creek, E side of Ebbett's Pass on hwy 4, 2 km E of summit, 2350 m, 17 Jul 1977, JTS 77G39, *P. c. murrayana,* (apt., alat.); W side of Ebbett's Pass on hwy 4, 18 km W of summit, 2470 m, 17 Jul 1977, JTS 77G44, *P. c. murrayana,* (apt.). *EL DORADO Co.:* South Lake Tahoe, 1950 m, 16 Jul 1977, JTS 77G31, *P. c. murrayana,* (apt., alat.); Upper Echo Lake, 2400 m, 6 Aug 1937, E. O. Essig. *P. c. murrayana,* (apt.); Wright's Lake, 850 m, 28 Sep 1969, C. Lagace, *Pinus* sp., (ovip.). *INYO Co.:* Bishop, 15 Sep 1969, T. Kono & M. Wasbauer, CDFA 69-J30-32, *P. c. murrayana,* (apt.); Lake Sabrina, nr Bishop, 2750 m, 1 Aug 1977, JTS 77H1, *P. c. murrayana,* (apt., alat.). *MONO Co.:* 7 km S of Crestview on hwy 395, 1 Aug 1977, JTS 77H5, *P. c. murrayana,* (apt.); Deadman Summit on hwy 395, nr Crestview, 2440 m, 31 Jul 1977, JTS 77G71, *P. c. murrayana,* (apt.). *NEVADA Co.:* Prosser Lake Recreation Area, hwy 89, 25 Jun 1977, JTS 77F6, *P. c. murrayana,* (apt.). *PLUMAS Co.:* 13 km E of Chester on hwy 36, 1520 m, 4 Jul 1977, JTS 77G14, *P. c. murrayana,* (apt., alat.); hwy 36, 8 km W of jct with hwy 89, 1460 m, 10 Jul 1977, JTS 77G24, *P. c. murrayana,* (apt.). *SIERRA Co.:* 18 km S of Sierraville on hwy 89, 26 Jun 1977, JTS 77F8, *P. c. murrayana,* (apt.); Donner Summit on hwy 80, 2200 m, 27 Aug 1978, JTS 78H159, *P. c. murrayana,* (apt.); same but 2290 m, 25 Jun 1977, JTS 77F3, *P. c. murrayana,* (apt.). *SISKIYOU Co.:* Edson Creek access Rd, Shasta Natl Forest, 8 km W of Bartel on hwy 89, 1160 m, 3 Jul 1977, JTS 77G9, *P. c. murrayana,* (apt.). *TULARE Co.:* 8 km NW of Stoney Creek Cmpgd, Sierra Natl Forest, 2380 m, 13 Aug 1977, JTS 77H11, *P. c. murrayana,* (apt., alat.). *TUOLUMNE Co.:* Yosemite Natl Park, Tuolumne Meadows, 22 Aug 1955, J. MacSwain, *P. c. murrayana,* (apt.); same but nr Porcupine Flat-Porcupine Creek, 2500 m, 30 Jul 1977, JTS 77G66, (apt.). *COUNTY UNCERTAIN:* Lake Tahoe, 16/17/21 Jul 1969, R. Luck, *P. c. murrayana,* (apt., alat.).

KEY TO THE VIVIPAROUS APTERAE OF *ESSIGELLA*

Before using this key, see the commentary under taxonomic key usage in the methods section; also see the character discussion section.

1a. 　Abdominal terga III–IV each with 6 dorsal (major + minor) setae between muscle attachment plates (e.g., Fig. 1F). 23

1b.   Abdominal terga III–IV each with 7 or more dorsal (major + minor) setae between muscle attachment plates. 2

2a.   (1b) Pro- *and* metatibiae subtly to conspicuously darker than mesotibiae, with mesotibial pigmentation approximately that of abdominal terga, or paler. Abdominal tergum VIII with 8 or more setae. Lateral-most minor dorsal seta on each side, between muscle attachment plates on abdominal terga III–IV, usually conspicuously anterad of immediately mesad neighbor (e.g., Figs. 1C–D). ... [pigmented *E.* (*Lambersella*)]   17

2b.   All tibiae concolorous, or metatibiae darker than pro- and mesotibiae. Setae on abdominal tergum VIII and arrangement of dorsal (major + minor) setae on abdominal segments III–IV variable (e.g., Figs. 1B–E). 3

3a.   (2b) Abdominal tergum I fused to the amalgamated meso + metanota; this fusion at least along their lateral contacts, but may be dorsally complete in more heavily pigmented specimens. .. *E.* (*E.*) *essigi* Hottes (Host: *P. radiata, P. attenuata*)

3b.   Abdominal tergum I always completely free. 4

4a.   (3b) Metadistitarsal length usually > 2.0 (rarely to 1.9) × length of meta-basitarsus (*if 1.9–2.0×, then*: color in life of vivip. apt. is pale yellow, oviparae with abdominal terga II–VII fused). Slide-mounted specimens always concolorously pale. .... *E.* (*A.*) *kathleenae* Sorensen (Host: *P. lambertiana*)

4b.   Metadistitarsal length at most 1.95×, usually less, length of metaba-sitarus (*if 1.9–2.0×, then*: color in life of vivip. apt. is usually not pale yellow, oviparae with abdominal terga II–VI fused but VII free, host *P. flexilis* or *P. strobiformis*). Slide-mounted specimens variable, pale to developed pigmentation of some sort. 5

5a.   (4b) Primary rhinarium on antennal segment V close to tip; distance between distal portion of rim of primary rhinarium and tip < 0.5, usually < 0.3, × diameter of rhinarium. Distal face of rim of primary rhinarium extending perpendicularly to longitudinal axis of segment V. Membrane of primary rhinarium, if extended, often reaching tip of segment. .... *E.* (*E.*) *wilsoni* Hottes (Host: *Pseudotsuga menziesii, Pseudotsuga macrocarpa*)

5b.   Distal rim of primary rhinarium and tip of antennal segment V more distant than 0.5× diameter of primary rhinarium. Distal face of rim of primary rhinarium usually extending obliquely from antennal segment. Membrane of primary rhinarium, when protruding, not reaching tip of segment. 6

6a.   (5b) Abdominal tergum VIII bearing 6, occasionally 7, setae. 14

6b.   Abdominal tergum VIII with 8 or more setae. 7

7a.   (6b) Metadistitarsal length > 1.70× length of metabasitarsus (*if 1.9–2.0×, see couplet 4b*). Slide-mounted specimens always concolorously pale. .... *E.* (*A.*) *kirki* Sorensen (Host: *P. flexilis, P. strobiformis*)

7b.   Metadistitarsal length < 1.70× length of metabasitarsus. Side-mounted specimens with variable pigmentation, pale to developed. 8

8a.   (7b) Abdominal terga III–IV each with 8 dorsal (major + minor) setae

in *1 roughly linear row* (but occasionally with the pair of setae immediately lateral to the most mesal pair displaced anterad) so that the lateral-most minor dorsal seta on each side of these terga is *not conspicuously anterad* to its immediately mesad neighbor (e.g., Fig. 1E). 9

8b. Abdominal terga III–IV each with 8 or more dorsal (major + minor) setae in *2 rows or staggered,* so that the lateral-most minor dorsal seta on each side is *conspicuously anterad* to its immediately mesad neighbor (e.g., Figs. 1B–C). 10

9a. (8a) Adult apterae with 2 marginal setae on abdominal segments III–IV. Mesonotum of later stadia nymphs of apterae with area immediately surrounding muscle attachment sites membranous; bases of neighboring setae not on a sclerotized plate contiguous with the muscle attachment sites. .... *E. (E.) alyeska* Sorensen
(Host: *Picea glauca, Pinus banksiana*)

9b. Adult apterae with 3 or more marginal setae on abdominal segments III–IV. Mesonotum of later stadia nymphs of apterae with sclerotization (light to dark pigmentation) extending from muscle attachment sites to form a pair of contiguous plates (approximately the diameter of the eye length) that engulf some neighboring setal bases. 10

10a. (8b, 9b) Ventral abdominal sclerites on segments III–IV linear to sublinear (when not folded), the length (anteroposterior axis) of longest sclerite > 2.0× width (mesolateral axis). . [some *E. (Lambersella)*]   17

10b. Ventral abdominal sclerites on segments III–IV circular to subcircular (when not folded), the length of longest sclerite, < 2.0, usually < 1.5× width. 11

11a. (10b) At least some setae on frons and some dorsal setae on central one-third of metafemora and metatibiae with sharp tips. ....
.... [some *E. (Lambersella)*]   17

11b. Tips of all setae on frons and all dorsal setae on central one-third of metafemora and metatibia incrassate. 12

12a. (11b) Dorsal setae on metatibiae with an abrupt transition in length (nearly doubling) about midway along segment. ....
.... [some *E. (Lambersella)*]   17

12b. Dorsal setae on metatibiae approximately equal in length or gradually increasing distally. 13

13a. (12b) Body dorsum dark with a longitudinal paler region on dorsomedial region of thoracic and abdominal terga. ... [some *E. (Lambersella)*]   17

13b. Body dorsum pale to dark, *but if dark then* either concolorous or frontal area of head is paler than abdominal dorsum. 14

14a. (6a, 13b) Mesonotum of later stadia nymphs of apterae with a pair of light to dark pigmented sclerotizations that extend from muscle attachment sites to form contiguous plates that engulf some neighboring setal bases; the diameter of these plates approximates the eye length. Adult apterae with pigmentation of body dorsum variable, often thoracic and abdominal terga are dark brown to black; *if pale (nonteneral) then*: (a) ventral abdominal sclerites on segments III and IV conspicuous, circular or subcircular (when not folded), and large (minimum

diameter at least 0.6× metatibial diameter); (b) antennal segment III length usually > 0.160 mm; (c) maximal distal diameter of extended siphuncular flange usually < 0.040 mm; and (d) 3–4 marginal setae on abdominal terga III–IV. . . . . [*E. (E.) knowltoni* complex]   15

14b. Mesonotum of later stadia nymphs of apterae with only membranous areas immediately surrounding muscle attachment sites; bases of neighboring setae not on contiguous sclerotized plates with the muscle attachment sites. Adult apterae with thoracic and abdominal terga pale and: (a) ventral abdominal sclerites segments III and IV variable, frequently small with minimum diameter < 0.6× metatibial diameter; (b) antennal segment III length < 0.160 mm; (c) maximal distal diameter of extended siphuncular flange usually > 0.040 mm; and (d) abdominal terga III–IV with 2 marginal setae. . . *E. (E.) alyeska* Sorensen
(Host: *Picea glauca, Pinus banksiana*)

15a. (14a) Darkest pigmentation (nonteneral) of antennal segments III, IV, and V subtly to substantially lighter than antennal segment I. Antennal segment III pale except distal one-quarter frequently slightly pigmented. Body dorsum, including frons, uniformly dark brown to black. Longest dorsal seta on central one-third of metatibiae usually < 0.8, rarely > 1.1,× metatibial diameter. Maximum distal diameter of extended siphuncular flange usually > 0.040 mm. . . . .
. . . . *E. (E.) critchfieldi* NEW SPECIES
(Host: *P. contorta contorta*)

15b. Darkest pigmentation (nonteneral) of antennal segments III, IV, and V darker than antennal segment I. Distal one-third to one-half of antennal segment III dark. Body dorsum variable; if dark, frons often lighter than abdominal dorsum. Longest dorsal seta on central one-third of metatibiae variable, often > 1.1× metatibial diameter. Maximum distal diameter of extended siphuncular flange usually < 0.040 mm. . . . . [*E. (E.) knowltoni*]   16

16a. (15b) Body dorsum usually moderately to extremely dark, occasionally pale; when dark, frons often lighter than abdominal dorsum; when pale, the ventrolateral border of abdominal tergum, anteroventral border of frons, and posterad border of subgenital plate well defined and demarcated from adjacent membranous regions. Abdominal tergum VIII with 6, rarely to 8, setae. *E. (E.) knowltoni knowltoni* Hottes
(Host: *P. contorta latifolia*; *P. contorta murrayana* [Oregon])

16b. Body dorsum usually pale to infrequently moderately dark; not extremely dark. Darker specimens with frons concolorous with abdominal dorsum; and with either the ventrolateral border of abdominal tergum, anteroventral border of frons, or posterad border of subgenital plate usually poorly defined compared to adjacent membranous regions. Abdominal tergum VIII with 5–8, rarely to 10, setae. . . . .
. . . .*E. (E.) knowltoni braggi* Hottes
(Host: *P. contorta murrayana* [California])

17a. (2a, 10a, 11a, 12a, 13a) Background of body dorsum darker than tibiae, with a paler longitudinal area on dorsomedial region of the thoracic and abdominal terga. . . . . *E. (L.) eastopi* NEW SPECIES
(Host: *P. coulteri*)

17b. Background of body dorsum variable from uniformly pale to dark, or mottled, but not as described in couplet 17a; *if dark then* lacking a paler longitudinal area on dorsomedial region of thoracic and abdominal terga, and pro- and metatibiae substantially pigmented. 18

18a. (17b) Length of dorsal setae on central one-third of metatibiae > 0.100 mm, *and* metatibial length < 0.905 mm. Tips of these setae sharp, often reflexed. 22

18b. Length of dorsal setae on central one-third of metatibiae < 0.100 mm, *or* metatibial length > 0.905 mm. Tips of these setae variable, incrassate to sharp, but not reflexed. 19

19a. (18b) Metatibial length > 1.30 mm, *and* antennal segment III length > 0.200 mm, *and* head width (noncompressed slide) measured at lateral bases of antennae > 0.330 mm   *E. (L.) hillerislambersi* NEW SPECIES (Host: *P. jeffreyi*)

19b. Metatibial length < 1.30 mm, *or* antennal segment III length < 0.200 mm, *or* head width (noncompressed slide) measured at lateral bases of antennae < 0.330 mm [default here if unsure of degree of slide compression]. 20

20a. (19b) Discriminant score (D.S.) < −1.2769,
　　　where D.S. =
　　　　　　[(antennal segment III length in mm)× (−41.1157)]
　　　　+　[(antennal segment IV length in mm)× (−71.1238)]
　　　　+　[(antennal segment V in mm)× (50.8637)]
　　　　+　[(eye length in mm)× (−58.8556)]
　　　　+　[(number of dorsal {major + minor} setae on abdominal tergum
　　　　　　III)× (0.5209)]
　　　　+　(9.81618). .... *E. (L.) hillerislambersi* NEW SPECIES
　　　(Host: *P. jeffreyi*)

20b. D.S. (couplet 20a) > −1.2769. 21

21a. (20b) Discriminant score (D.S.) > 1.3945,
　　　where D.S. =
　　　　　　[(metatibial length in mm)× (−8.3479)]
　　　　+　[(metabasitarsal length in mm)× (−63.4133)]
　　　　+　[(antennal segment III length in mm)× (65.4496)]
　　　　+　[(dorsomedial length of head + pronotum in mm)× (−29.4826)]
　　　　+　[(dorsomedial length of abdominal tergum I in mm)× (38.7739)]
　　　　+　(12.4544). .... *E. (L.) eastopi* NEW SPECIES
　　　(Host: *P. coulteri*)

21b. D.S. (couplet 21a) < 1.3945. .... [*E. (L.) fusca*]   22

22a. (18a, 21b) Discriminant score (D.S.) < −0.0803,
　　　where D.S. =
　　　　　　[(metabasitarsal length in mm)× (71.9890)]
　　　　+　[(length of longest dorsal seta on central part of metatibiae in
　　　　　　mm)× (−51.6627)]
　　　　+　[(number of dorsal {major + minor} setae on abdominal tergum
　　　　　　VIII)× (0.9549)]
　　　　+　[(length from anterior of eye to posterolateral corner of prothorax)× (−28.9019)]
　　　　+　[(length of longest seta on antennal segment II)× (−98.3813)]

+ (−6.11263). . . . . *E. (L.) fusca voegtlini* NEW SUBSPECIES
(Host: *P. ponderosa, P. jeffreyi, P. coulteri*)

22b. D.S. (couplet 22a) > −0.0803. . . . . *E. (L.) fusca fusca* G & P
(Host: *P. ponderosa, P. ponderosa* var. *arizonica, P. engelmannii, P. leiophylla*)

23a. (1a) Mesonotum of later stadia nymphs of apterae with area immediately surrounding muscle attachment sites membranous; bases of neighboring setae not on a pair of contiguous, sclerotized plates (light to dark pigmentation) extending from muscle attachment sites. Western Nearctic in distribution [default here if specimen is from the Rocky Mountains, Black Hills or westward, Mexico or not North American]. . . . . [*E. (E.) californica* complex]

23b. Mesonotum of later stadia nymphs of apterae with sclerotization (light to dark pigmentation) extending from muscle attachment sites to form a pair of contiguous plates (approximately the diameter of the eye length) that engulf some neighboring setal bases. Eastern Nearctic in distribution [default here if specimen is from east of the Rocky Mountains or Black Hills and not Mexico]. . . . . *E. (E.) pini* Wilson
(Host: most eastern *Pinus* sp.)

24a. (23a) Siphunculi conspicuously darker than surrounding abdominal terga, or dorsal (major + minor) setae between muscle attachment plates on abdominal terga II–VI, on dark basal scleroites with well defined borders (nonnymph). . . . . *E. (E.) californica* (Essig)
(Host: most *Pinus* sp. [except pinyons])

24b. Siphuncular pigmentation approximately equivalent to surrounding abdominal terga. Dorsal (major + minor) setae between muscle attachment plates on abdominal terga II–VI arising from undifferentiated areas of abdominal terga, or from areas that are subtly darker, but have only vaguely defined borders. 25

25a. (24b) Abdominal terga (excluding tergum immediately adjacent to setal bases) subtly to conspicuously darker than thoracic terga and head dorsum. . . . . *E. (E.) hoerneri* G & P
(Host: *P. monophylla, P. edulis, P. cembroides, P. quadrifolia*)

25b. Abdominal terga (excluding tergum immediately adjacent to setal bases) concolorous with thoracic and head terga; if body dorsum pigmented, abdominal terga not contrasting with thoracic terga and head dorsum. 26

26a. (25b) Slide compressed or sagittal plane of aphid rolled from vertical axis; body width measurements potentially distorted by compression or perspective artifacts of slide preparation [default here if uncertain]. 27

26b. Slide not compressed and sagittal plane of aphid not rolled; body width measurements not distorted by compression or perspective artifacts of slide preparation. 28

27a. (26a) Discriminant score (D.S.) > 0.3991,
where D.S. =
[(antennal segment IV length in mm)× (0.0093)]
+ [(antennal segment II length in mm)× (−0.1345)]

+ [(stylet length in mm)× (0.0134)]
+ (0.39912). .... *E. (E.) hoerneri* G & P
   (Host: *P. monophylla, P. edulis, P. cembroides, P. quadrifolia*)
27b. D.S. (couplet 27a) < 0.3991. .... *E. (E.) californica* (Essig)
   (Host: most *Pinus* sp. [except pinyons])
28a. (26b) Discriminant score (D.S.) < −0.4847,
   where D.S. =
        [(antennal segment IV length in mm)× (0.0059)]
   + [(antennal segment II length in mm)× (0.2023)]
   + [(head width at lateral base of antennae in mm)× (−0.0456)]
   + [(stylet length in mm)× (−0.0083)]
   + (3.18802). .... *E. (E.) hoerneri* G & P
   (Host: *P. monophylla, P. edulis, P. cembroides, P. quadrifolia*)
28b. D.S. (couplet 28a) > −0.4847. .... *E. (E.) californica* (Essig)
   (Host: most *Pinus* sp. [except pinyons])

PHYLOGENETIC ANALYSES: $t\bar{I}$

During this project, the need for development of an operational method to estimate phylogeny using noncoded, morphometric attributes became apparent, because *Essigella* have few morphological traits that could be treated or coded objectively using the then existing numerical cladistic procedures that were based upon discrete-state data. While analyzing the genus (Sorensen 1983), I developed a phylogenetic procedure for morphometric data that employed discriminant function analysis to reveal unshared variance among groups, and then linked the group centroids to yield a phylogenetic network. That procedure was later modified (Sorensen 1987a) to yield the currently accepted phylogeny for the genus. The method estimates minimum selective mortality indices (sensu Lande 1979) that account for divergence resulting from past selection (Pimentel 1992). Sorensen & Foottit (1992) present the quantitative genetic rationales for the procedure, and Sorensen (1992b) discusses its operational limitations.

The phylogeny developed for *Essigella,* as $t\bar{I}$ of Sorensen & Foottit (1992), Sorensen (1992b) and here [= β of Sorensen (1987a)], is based on adult virginoparous apterae only. Sorensen (1983) used 26 morphometric traits (see methods section) to derive $t\bar{I}$ and circumscribe all *Essigella* taxa; these are listed elsewhere (see Sorensen 1991: table 1). For *Essigella, $t\bar{I}$* was generated using discriminant function analysis (Nie et al. 1975: SPSS, version 7, program DISCRIMINANT, direct selection mode, Wilks-λ criterion) to derive group centroids, as mean group phenotypes ($\bar{z}$, sensu Lande 1979) for taxa; this was followed by their linkage using a maximum-likelihood cladistic algorithm (Felsenstein 1984: PHYLIP, version 2.5, program CONTML, c-option); the analysis included *Pseudessigella,* as an outgroup (Sorensen 1990), for rooting. Because this phylogenetic estimate is probability based, as a maximum-likelihood network, confidence intervals for each phyletic segment (internode) were generated; these are listed in Sorensen (1987a: table 1).

In Fig. 13, $t\bar{I}$ is shown with the length of its internodes, which represent evolved apomorphic anagenic distance, scaled proportionally to their divergence. Figure 14 shows this phylogenetic pathway as it navigates through the 3-dimensional
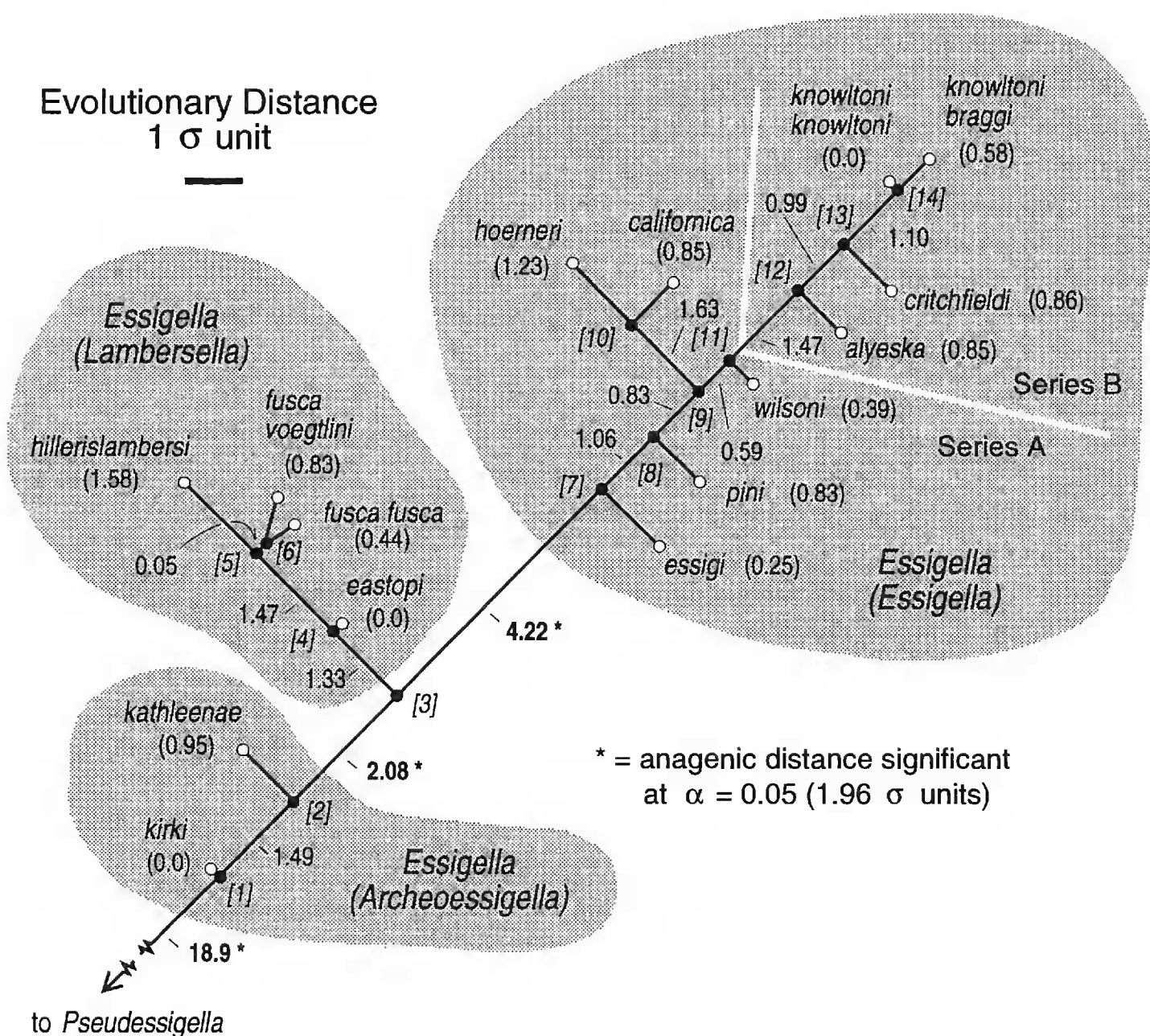
Figure 13. Anagenic distance preserving portrayal of the phylogenetic estimate, $t\bar{I}$, for *Essigella* (after Sorensen 1987a). White nodes are taxa (as group centroids); black nodes (numbered in square brackets) are ancestors; internode lengths are proportionate to their anagenic distances (indicated) in pooled standard deviation units (σ); internodes that are significant (as > 1.96 σ for α = 0.05) for the genus/subgenus level are shown in bold numbers with an asterisk. Subgenera are indicated by shading.

discriminant space that is represented by the dominant three minimum selective mortality vectors (Sorensen & Foottit 1992, Sorensen 1992b) occurring over the given evolutionary episode. Although preserving the furcation patterns in that space, Fig. 14 necessarily distorts the internodal distances, which are derived from the full 15 dimensions (= Groups − 1) of the data matrix. The cladistic relationships among *Essigella* species should be obvious from these figures; for discussion, see Sorensen (1992b) or Sorensen (1987a).

Justification for Delimitation of Subgenera. — Because *Pseudessigella* was necessarily included in the analysis for polarity, and because it represents the nearest separate genus (Sorensen 1990), the analytical perspective (sensu Sorensen 1992b) used in generating $t\bar{I}$ allows inference of reasonable, quantitatively determined subgeneric demarcations within *Essigella*. This is possible, and logically called for, because, for the general analytical procedure:

(1) All, and only, unshared variance (apomorphy, sensu Sorensen & Foottit 1992) among the taxa is used in network construction, so that the derived inter-
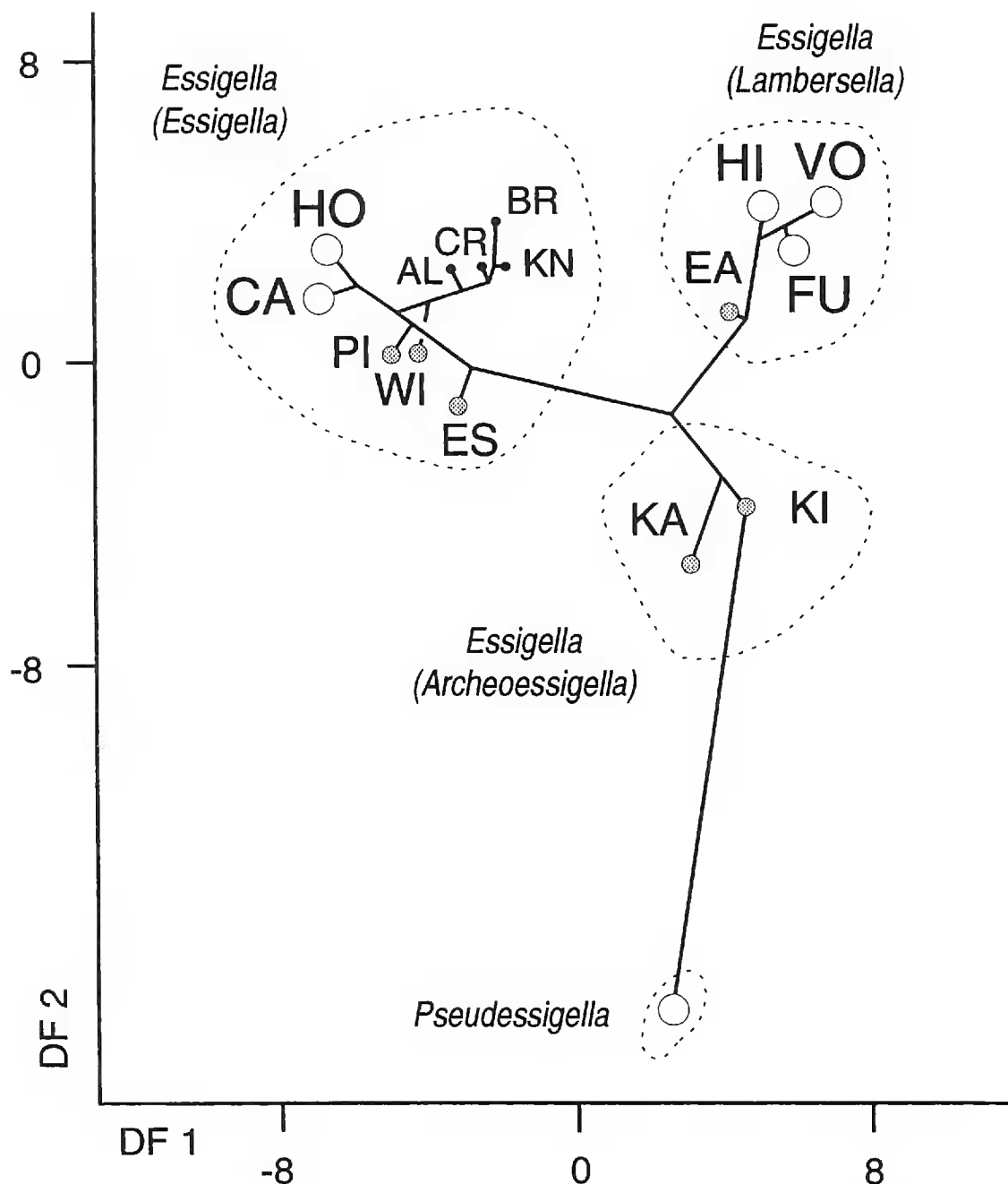
Figure 14.   Spatial-based portrayal for $t\bar{I}$ (after Sorensen 1992b). Here, $t\bar{I}$ transverses the evolutionary space defined by the dominant three minimum selective mortality vectors (sensu Lande 1979), represented as discriminant functions (DF) (see Sorensen & Foottit 1992, Sorensen 1992b). Taxa (as group centroids) are abbreviated by their first two letters; the subgenera and *Pseudessigella* are circumscribed by dashed lines that indicate the maximal spatial distributions of their contained individuals. The first two vectors (DF1, DF2) are shown, and the third (DF3) is implied by the relative size and color of the dot, and size of letters, for each taxon: larger (white) dots are forward of, intermediate (gray) dots are on, and smaller (black) dots are backward from, the plane of the page. Phyletic internodes here are not proportionate to their anagenic distances (as in Fig. 13), but spatially demonstrate the furcation events in this evolutionary space.

node values appropriately portray a maximum-likelihood representation of solely apomorphic anagenic distance among the network nodes.

(2) The internodal lengths are in Mahalonobis' distance, as standard deviation units, σ [= SD units of Sorensen (1987a, 1992b)], that are parsimoniously pooled across all incorporated groups (as taxa). Thus, these σ distances have implied meaning for the relative levels of apomorphic divergence leading to the respective taxonomic ranks among all included taxa. In this case, divergence from both species and genus level taxa was incorporated. Because the former (16, including subspecies) were more numerous than the latter (2), the likelihood is that any given internode should represent a species-, rather than genus-, level divergence event.
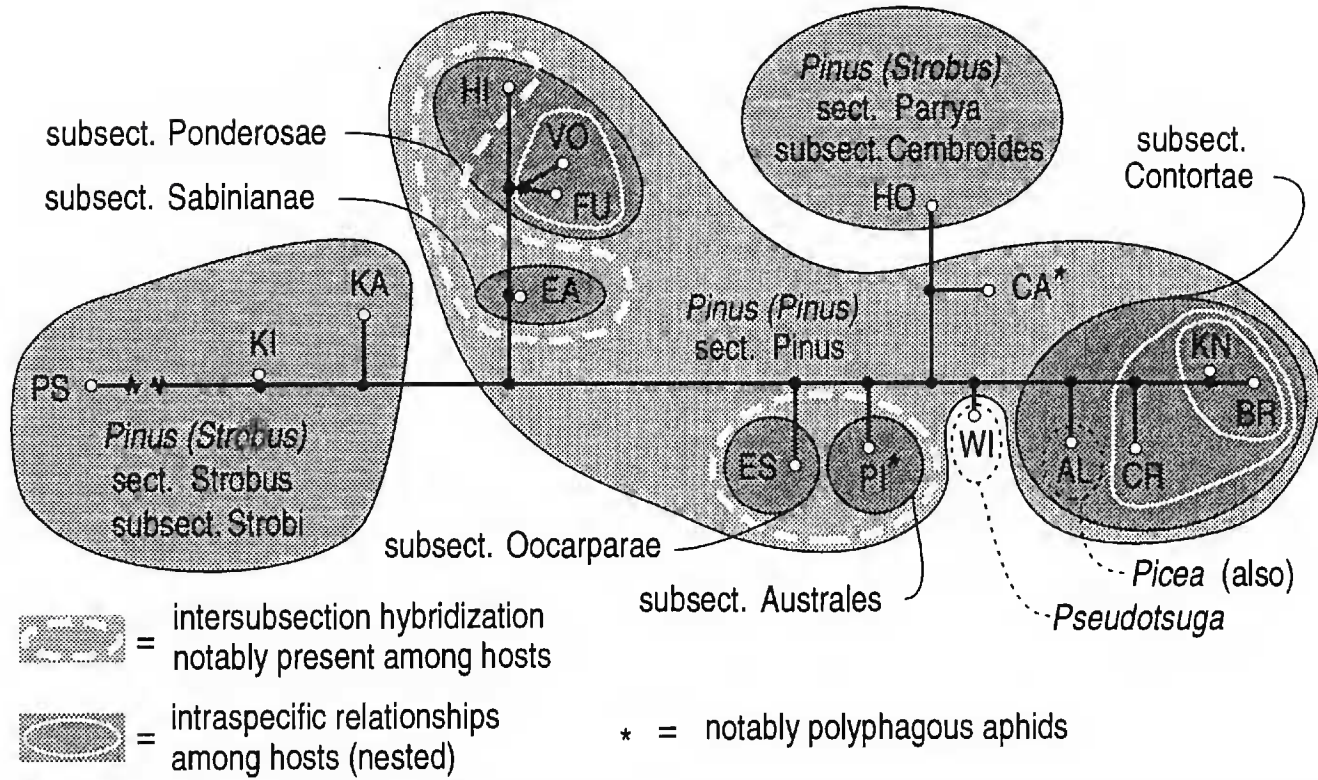
Figure 15. Diagrammatic portrayal of host plant radiation shown by *Essigella*. Here, $t\bar{I}$ is shown with preserved internodal anagenic distances, with evolution beginning at the left (see Fig. 13). Aphid taxa are designated by their first two letters. Host grouping to pine subsection are shown for the aphid taxa; where taxa are not strictly monophagous, they are assigned to the host group of their predominant pine species. Pine groupings follow Little & Critchfield (1969). Note that: (1) reinvasion of *Pinus* (*Strobus*) by *E.* (*E.*) *hoerneri* [HO] occurs in a separate section of that subgenus; (2) terminal groupings of the aphids occur within single pine subsections [e.g., Ponderosae, Contortae]; and (3) hybridization links between pine subsections mirror the evolutionary proximity of the aphids on $t\bar{I}$.

(3) The lengths of internodes on any $t\bar{I}$ network, in a large enough sample, should be Gaussian or Poisson in distribution. Therefore, because 95.45% of such lengths should occur within ±1.96 σ of the mean (Spiergel 1988: 90) in those distributions, an $\alpha = 0.05$ confidence level for significant differentiation in the length of any internode is appropriate at 1.96 σ (Spiergel 1988: 207). For any given relative perspective (sensu Sorensen 1992b), this should be true (i.e., if 15 genera, representing 3 tribes, were individual nodes on such a network, then internodes exceeding 1.96 σ should depict tribal level divergence); see Sorensen (1990) for discussion of similar objective taxonomic demarcations on networks.

Accordingly, on $t\bar{I}$, any internodal length exceeding 1.96 σ is significant in differentiation and, therefore, its divergence level exceeds the type most commonly encountered on this network: speciation. Such internodes indicate the next higher taxonomically recognizable level: genus (or subgenus, because these are functionally equivalent, sensu ICZN). Here, only three internodes exceed 1.96 σ; those between: *Pseudessigella* and node 1 (18.9 σ), nodes 2 and 3 (2.08 σ), and nodes 3 and 7, at (4.22 σ). They define the gaps between *Pseudessigella*, *E.* (*Archeoessigella*), *E.* (*Lambersella*), *E.* (*Essigella*), respectively. The gap between the existing genera is 18.9 σ; although the others are less, they are significant and reflect ecological divergence of the aphids onto host groups (see below), hence they are treated as subgenera. The subgeneric internode distances are not considered to represent species groups because *Pseudessigella* was included in the analysis; species group demarcation would have been appropriate if only *Essigella* taxa lacking subgeneric delimitation were analyzed.

Alternative Analyses. —Recently, PAUP (Swofford 1990) analyses were conducted, using on coded traits from *Essigella* apterae, nymphs, alates and oviparae (unpublished data); a majority rule consensus of the 150 PAUP minimum length trees supports the $t\bar{I}$ topology, with the following modifications: (a) the two *E. (Archeoessigella)* species form a basal trichotomy with the remaining clade, (b) *E. (E.) essigi* and *E. (E.) pini* form a sister clade [63%] to the remaining *E. (Essigella)*, and (c) *E. (E.) wilsoni* forms a trichtomy with the *E. (E.) californica /hoerneri* clade and Series B. These potential topological modifications, due to inclusion of additional morphs/stages, do not require altering the present subgeneric assignments. Because of space limitations here, these PAUP analyses will be published elsewhere.

ECOLOGICAL CORROBORATION OF PHYLOGENY

It is reasonable to assume that associated ecological and biogeographic information for the taxa should substantiate, or at least not refute, $t\bar{I}$ if indeed it approximates the correct phylogeny. Because of the apparent feeding specificity of *Essigella,* the hosts, principally pines, are assumed to be important to the interpretation of the aphids' evolution. A resource tracking model of evolution (Brooks 1981), seems at least partially applicable with lineages of *Essigella* shifting to, and sometimes evolving with, various lineages of pines or their relatives. Unfortunately, no cladistic evidence for a phylogeny of *Pinus* exists. In its absence, Little & Critchfield's (1969) revision of *Pinus* is used here and the evolutionary interrelationships among pines are assumed to mirror their genetic compatibilities, as shown through the extensive U.S. Forest Service hybridization programs (W. Critchfield, personal communications). Figure 15 shows a diagrammatic portrayal of the host radiation across pine subsections that has occurred during evolution within *Essigella*; this portrayal is superimposed over $t\bar{I}$.

Little & Critchfield (1969) divide the genus *Pinus* into three subgenera: *Ducampopinus, Strobus,* and *Pinus.* (The older terms haploxylon and diploxylon, previous subgeneric synonyms for *Strobus* and *Pinus,* respectively, are used here as adjectives.) Subgenus *Ducampopinus,* as a single southeast Asian species, is universally regarded as primitive (Mirov 1967). Subgenus *Strobus,* which shares some derived characters with subgenus *Pinus,* is regarded as more primitive than the latter (D. Axelrod, W. Critchfield, personal communications). Subgenus *Strobus* contains section Strobus, with subsections Cembrae and Strobi, and section Parrya, with subsections Cembroides, Gerardianae* and Balfourianae. Subgenus *Pinus* contains section Ternatae, with subsections Leiophyllae, Canarienses* and Pineae*, and section Pinus, with subsections Sylvestres, Australes, Ponderosae, Sabinianae, Contortae and Oocarpae. Those subsections with an asterisk (*) have no Nearctic native species; subsections Cembrae and Sylvestres are predominantly nonNearctic.

The only *Essigella* species restricted to the primitive subgenus *Strobus,* with the exception of *E. (E.) hoerneri* (discussed later), are *E. (A.) kathleenae,* on *P. lambertiana,* and *E. (A.) kirki,* on *P. flexilis* and *P. strobiformis*; both aphids are in *E. (Archeoessigella)* and both pines are in subsection Strobi (Fig. 15). *Pinus flexilis* and *P. strobiformis* are closely related and occupy nearly allopatric zones interfacing at the Colorado-New Mexico border. *Pinus strobiformis* was previously treated as a variety of *P. flexilis,* and intergrades with it in sympatry (Critchfield

& Little 1966). *Pinus lambertiana* is distinctive among haploxylon pines and is genetically incompatible with most of them; it is compatible, however, with *P. griffithi*, an Asian subsection Strobi pine that is restricted to the Himalayas and is the host of *Pseudessigella brachychaeta*, *Essigella*'s sister-group (Sorensen 1991). The more advanced *Essigella* subgenera, *E.* (*Lambersella*) and *E.* (*Essigella*) [except *E.* (*E.*) *hoerneri*], occur on pines of the derived subgenus *Pinus*, or on other Pinaceae genera, when host specific (Fig. 15).

Within *E.* (*Lambersella*), *E.* (*L.*) *fusca* occurs primarily on *P. ponderosa*, but also on *P. engelmannii*, as *E.* (*L.*) *f. fusca*, and on *P. jeffreyi* and *P. coulteri*, as *E.* (*L.*) *f. voegtlini*. *Essigella* (*L.*) *hillerislambersi* and *E.* (*L.*) *eastopi* are monophagous on *P. jeffreyi* and *P. coulteri*, respectively. *Pinus ponderosa*, *P. jeffreyi* and *P. engelmannii* are in subsection Ponderosae, and all hybridize. *Pinus coulteri* is in subsection Sabinianae, but hybridizes with *P. jeffreyi*, although not with *P. ponderosa*. Consequently, the *tī* furcation pattern within *E.* (*Lambersella*) mirrors the *P. coulteri* to *P. jeffreyi* to *P. ponderosa* hybridization link (Fig. 15 [where, note the HI vs FU/VO positions could be rotated]). Furthermore, subsection Ponderosae is genetically distinct and divergent within subgenus *Pinus*, and its species show little hybridization with pines in other subsections (W. Critchfield, personal communication). Therefore, the divergence of that pine subsection reflects that of *E.* (*Lambersella*), as a clade, from *E.* (*Essigella*), which primarily occupies the other Nearctic diploxylon pine subsections (Fig. 15).

Among Series A taxa (Fig. 13) within *E.* (*Essigella*), when host specificity is restricted, the hosts have austral biogeographic origins during the Madro-Tertiary geoflora (Alexrod 1958, 1967). On *tī*, which was based solely on morphometric attributes from apterae, the phylogenetic topology indicates a paraphyletic relationship between *E.* (*E.*) *essigi* and *E.* (*E.*) *pini*, as the more primitive taxa in the subgenus. *Essigella* (*E.*) *essigi*'s hosts, *P. radiata* and *P. attenuata* of subsection Oocarpae, interbreed. *Essigella* (*E.*) *pini*, in the eastern Nearctic, feeds widely in subsection Australes and also in subsection Strobi; the latter probably are secondary adaptations to unoccupied niches in the east. Subsections Australes and Oocarpae have a strong hybridization link (Fig. 15) that temporally reflects the phylogenetic proximity of these aphids. Thus, evidence suggests that this most primitive section of *E.* (*Essigella*) probably originated in association with the Madro-Tertiary geoflora, where its immediate aphid ancestor probably fed on the pine ancestor to both the Australes and Oocarpae subsections. Under this scenario, and *E.* (*E.*) *essigi* and *E.* (*E.*) *pini* probably diverged on Oocarpae pines in the western Nearctic and Australes pines in the eastern Nearctic, respectively, as those pines moved north.

The phylogenetic analyses indicate that *E.* (*E.*) *californica* and *E.* (*E.*) *hoerneri* form a monophyletic subunit. In that clade, *E.* (*E.*) *hoerneri* is restricted to section Parrya subsection Cembroides (pinyon pines), which have their greatest diversity in the southern Nearctic. This host specificity is probably a secondary invasion of unoccupied haploxylon niches (Fig. 15). In contrast, *E.* (*E.*) *californica* feeds broadly in *Pinus*, but not on pinyons, presumably because of competition there from *E.* (*E.*) *hoerneri*. The remaining Series A taxon, *E.* (*E.*) *wilsoni*, is the sister-group to Series B (Fig. 13). That aphid feeds on *Pseudotsuga*, again a host of southern Nearctic origin, and which apparently represents another secondary adaptation to an unoccupied niche (Fig. 15).

The Series B aphid lineage (Fig. 13) most probably has an origin in the Arcto-Tertiary geoflora (Sorensen 1992a). Although *E. (E.) alyeska* again shows another secondary adaptation of host by using *Picea glauca,* it also feeds on *Pinus banksiana,* an eastern subsection Contortae pine (Fig. 15). That pine subsection is the host of *E. (E.) alyeska*'s sister-group, the *E. knowltoni* complex, whose aphid and host relationships are detailed in Sorensen (1992a). Within the complex, the most distinct aphid, *E. (E.) critchfieldi,* feeds on *P. contorta contorta,* which is the more distantly related and distinctive of the occupied *P. contorta* subspecies; in contrast, *E. (E.) knowltoni knowltoni* and *E. (E.) knowltoni braggi,* as subspecies, occupy the *Pinus contorta latifolia-murrayana* subspecies cline (Fig. 15).

Thus, host associations, their genetic compatibilities and their suspected biogeographic origins, all tend to corroborate at least the greater aspects of the *tĪ* phylogeny for *Essigella.* If that scenario is correct, *Essigella* originated on subgenus *Strobus* pines, and radiated, as a clade, onto those of the subgenus *Pinus* in the Madro-Tertiary geoflora. That clade split soon after its inception. A morphologically more plesiomorphic daughter clade moved onto, or evolved with, pines of subsections Sabinianae and Ponderosae. A morphologically more derived daughter clade moved onto pines of subsections Oocarpae and Australes, which moved north in the eastern and western Nearctic, respectively, over geologic time. The latter clade continued to radiate in the western Nearctic, seeking unoccupied niches, and among its species: one secondarily reinvaded subsection Cembroides of subgenus *Strobus,* one colonized *Pseudotsuga,* and a monophyletic lineage invaded subsection Contortae pines in the Arcto-Tertiary geoflora.

Ecologically, single species of *Essigella* in the east and west, each have evolved relative polyphagy, probably to exploit niches with no or limited competition. Niche competition is seen as a driving force in *Essigella*'s evolution, because several apparent instances of character displacement seem to occur within its species complexes (Sorensen 1992a, unpublished data). Interestingly, only one, albeit relatively polyphagous, *Essigella* exists in the eastern Nearctic. That species, *E. (E.) pini,* appears to necessarily feed chiefly on subsection Australes, which is the predominant diploxylon pine group there. Records indicate that it also feeds in subsections Strobi (subgenus *Strobus*), Sylvestres and Contortae, although the latter is occupied by *E. (E.) alyeska* in the northeastern Nearctic. More *Essigella* species may have failed to develop in the eastern Nearctic, where subsection Australes predominates, because of the lack of pine subsection diversity in that area, in contrast to the west. In the west, *E. (E.) californica* seems to feed on nearly all pine subsections except Cembroides, which its very close sister, *E. (E.) hoerneri,* occupies; in fact, my collections of *E. (E.) californica* on pines of any given subsection were considerably lessened if that host group had a monophagous, closely related, *Essigella* occupant.

Among the Nearctic pine groups, the only one not occupied by *Essigella* is the haploxylon subsection Balfourianae (Sorensen 1983). Those subgenus *Strobus* pines are generally considered to be evolutionary relicts that are restricted to small, scattered, high alpine regions (Critchfield & Little 1966). Despite my numerous attempts, *Essigella* has not been found on Balfourianae pines, although *Cinara,* a more primitive Lachninae aphid genus (Sorensen 1990), does feed on them. This, along with the occurrence of *Pseudessigella* and *E. (Archeoessigella)* on relatively more advanced subsection Strobi pines, suggests that the Balfour-

ianae subsection of haploxylon pines may be older than *Essigella*. If so, then *Essigella* probably evolved in the mid-Tertiary, when *Pinus* was originating or radiating.

CONCLUSIONS AND SUGGESTIONS FOR FUTURE WORK

This revision recognizes 13 species, two subspecies, and three subgenera. Of these, three species, one subspecies, and two subgenera are described here as new; 13 of the 21 previous species names are synonymized and one is given lower status. I feel the framework of this revision is well corroborated, because the currently recognized intrageneric taxa reflect closely the genetic relationships of their Pinaceae hosts, and are strongly concordant with their known variation and suspected phylogenetic and biogeographic relationships. However, at present only the most common morph, the viviparous apterae, can be accurately keyed within the genus. Alates of many species cannot be identified with certainty and some morphs of most species remain unknown. Furthermore, the *Essigella* fauna of Mexico and its variation are largely unknown, although the pine diversity in that area is the greatest for any world region. Specimens seen from Mexico thus far, however, fit into the current classification without incident, and I intuitively suspect few, if any, new species will be found there, because most Mexican pine groups (subsections) exist and have been sampled further north.

New species might be anticipated, however. Hence, it is important to note the characters that are most likely to reflect important taxonomic differences among *Essigella* species or species groups. These are the ranges of variation or expression of: (a) pigmentation of the adult viviparous apterae, (b) the pattern and numbers of hairs on the abdominal dorsum, (c) the ventral abdominal sclerites on segments III–IV, (d) the sclerotization and fusion of the abdominal dorsum of oviparae, (e) the sclerotization of the mesonotum of later stadia nymphs of viviparous apterae, (f) the dorsal hairs on the metatibiae, and (g) the variation of the medius of alates. A recommendation for future work is that only adult viviparous apterae be considered for description of new species, and especially for holotype designation. Designation of an alate as a holotype should be avoided in particular [a major and problematic failing of Hottes (1957)].

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